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Family Pseudolividae (Caenogastropoda, Muricoidea): A polyphyletic taxon*

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de São Paulo, Cx. Postal 42494, 04299-970 São Paulo, SP, Brazil, lrsimone@usp.br

Abstract: A detailed morphological study was performed on the following taxa normally considered to belong to the family Pseudolividae: (1) *Zemira australis* (Sowerby, 1833) from Australia; (2) *Fulmentum ancilla* (Hanley, 1859) from South Africa; and (3) *Melapium lineatum* (Lamarck, 1822) from South Africa. Two additional species of pseudolivids, *Benthobia atafona* Simone, 2003 and *B. complexirhyna* Simone, 2003, from Brazil and New Zealand respectively, are considered. Two other muricoideans are included in this study: (1) *Nassodonta dorri* (Watteblet, 1886) [Nassariidae] from Vietnam (morphological study also included) and (2) *Siratus senegalensis* (Gmelin, 1791) (Muricidae) from Brazil (published elsewhere). Both species are outgroups, but operationally included as part of the ingroup in order to test the monophyly of the Pseudolividae. In particular, *N. dorri* has a shell very similar to a pseudolivid. A complete taxonomical and morphological treatment of each species is included, as a scenario of a formal phylogenetic analysis. Additional outgroups considered include a pool of Tonnoidea (the root) and Conoidea. The cladogram is: (Tonnoidea (Conoidea ((*Benthobia atafona–B. complexirhyna*) (*Nassodonta dorri* (*Zemira australis* (*Fulmentum ancilla* (*Siratus senegalensis–Melapium lineatum*))))))). Analyses of each important character and of the cladogram were performed. Some of the conclusions include that the family Pseudolividae, as presently understood, is polyphyletic, as it would include a nassariid (*N. dorri*) and a muricid (*S. senegalensis*).

Key words: Neogastropoda, polyphyly, morphology, phylogeny

The taxon Pseudolividae Fisher, 1884, had been previously used by several researchers (*e.g.*, Cossmann 1901, Golikov and Starobogatov 1975, Squires 1989), but it was better defined as a family by Kantor (1991), based on anatomical features of basal neogastropods. The family reunites genera previously considered as belonging to several other families, including, *e.g.*, Cancellariidae (*Benthobia* Dall, 1889), Buccinidae (*Buccinorbis* Conrad, 1865), and Olividae (*Melapium* Adams and Adams, 1853; *Pseudoliva* Swainson, 1840; *Sylvanocochlis* Melvill, 1903; *Zemira* Adams and Adams, 1853). This taxonomy was followed by some researchers (*e.g.*, Vermeij and DeVries 1997, Bouchet and Vermeij 1998, Pacaud and Schnetler 1999, Nielsen and Frassinetti 2003). Moreover, Vermeij (1997, 1998) revised the family Pseudolividae, including fossil species, establishing its origin in the late Cretaceous. A more complete history of the concept of the family can also be found in that paper. However, some authors still considered the family as a subtaxon of Olividae (*e.g.*, Hayes 1994, Smith 1998) (Pseudolivinae). Although our knowledge of pseudolivid species is relatively rich, particularly with regard to anatomy (*e.g.*, Ponder and Darragh 1975, Kantor 1991, Simone 2003), the definition of the family remains unclear, and no phylogenetic analysis has yet been performed, other than that of Kantor (1991).

The main difficulty in studying pseudolivids is finding preserved animals. Pseudolivids are normally rare and found in deep waters, which precludes obtaining a large set of samples for an extensive anatomical study. Although the pseudolivids are more abundant as fossils, with about a hundred species (Vermeij 1998), they are relatively poor in diversity in the Recent fauna, with about 10-15 living species. As about a third of the species are available for study, belonging to the different branches of the family, a study of them appears to be worthwhile, at least in terms of testing the monophyly of the group and identifying anatomical characters that would better define it.

This paper is part of a larger project on the phylogenetic definition of the Caenogastropoda based on detailed morphology, this time focusing the Pseudolividae. One of the genera, *Benthobia* Dall, 1889, was published elsewhere (Simone 2003), and the species of remaining genera are included herein.

Nassodonta dorri (Watteblet, 1886), from Vietnam, one of the few freshwater neogastropods known, belonging to the family Nassariidae, has a shell similar in morphology to those of pseudolivids (Kantor and Kilburn 2001). This taxon is also included in this study to test the monophyly of the Pseudolividae, as the shell characters certainly can converge.

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MATERIALS AND METHODS

Most specimens used in this study belong to institutional collections. The specimens were dissected by standard techniques, under a microscope, with the specimens immersed in water. Some organs such as the oviduct and foregut were processed by standard histological techniques to obtain serial sections 5 μm in thickness and stained using Mallory trichrome. Hard structures, such as shells, radulae, and jaws were also examined using the SEM in the "Laboratório de Microscopia Eletrônica do Museu de Zoologia da Universidade de São Paulo". The descriptive part of this paper provides a complete description of the first species; the remaining species are described under a comparative aspect, with most of similar features omitted. This measure is adopted for decreasing the length of this paper and for optimizing the data. The same approach is adopted in the figures. A detailed list of examined species follows each species description.

The section on comparative morphology is organized as a phylogenetic analysis. The account on each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s); also included are CI and RI (consistency and retention indices, respectively) and values for the character under the most parsimonious hypothesis. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. Hundreds of characters were selected, based on the examined samples. Those that emerged as autapomorphic, highly variable, or overlapping, were selected but not included in the cladistic analysis. The remaining characters were organized into states, coded, polarized comparing with outgroups, and a cladistic analysis was performed.

Other previously studied Caenogastropoda were selected as outgroups. They are mainly the following: Cerithioidea (Simone 2001), Stromboidea (Simone 2005), Cypraeoidea (Simone 2004a), Calyptraeoidea (Simone 2002), and architaenioglossans (Simone 2004b). In the discussion, some specific outgroup taxa are mentioned, based upon observed or published data. However, in the matrix of characters (Table 1) only 4 taxa are shown, the ground plan of the Conoidea and Tonnoidea. The ground plan of these superfamilies are chosen in the sense of being representative; however, the final result is the same if the ground plan were substituted by any one of the 64 (terminal) species present in those papers. Two additional species are included, *Siratus senegalensis* (Gmelin, 1790) [Muricidae], based on unpublished observations from another, ongoing study, and the nassariid *Nassodonta dorri*, mentioned above. Each character, state, and polarization is justified in the discussion section which includes a concise explanation when warranted.

The discussion of each character is also based on the analysis of the resulting tree (Figs. 1-2) although the matrix of characters (Table 1) and the subsequent tree (Figs. 1-2) are shown only in the following section.

The synapomorphies of the ingroup (superfamily autapomorphies) are preserved in the present paper, because they are the main concern as referred to in the introduction. The ingroup autapomorphies are the basis for a better establishment of a still imprecise taxon. They confirm the internal position of some possible "outgroups" such as tonnoideans and conoideans. They will be useful in the ongoing phylogenetic study of the entire order Caenogastropoda as the ground plan of the superfamily. Additionally, they are in agreement with some phylogenetic approaches used in studies of other groups (*e.g.*, Yeates 1992, Pinna 1996).

Some multistate characters are here analyzed under an additive (ordered) approach. In each case, the additive concept is justified in the discussion and is always based on the ontogeny, or because each state represents a clear modification of the preceding one. Additionally, each additive multistate character was also analyzed as non-additive, and any fortuitous change in the result and/or indices are also reported. The cladistic analysis was performed with the aid of the computer program "Tree Gardner 2.2" (Ramos 1997), which basically works as an interface of the Hennig86 (Farris 1988). The used algorithm was "ie". The computer program PAUP was also used, mainly to determine the robustness of the nodes. Both programs presented the same result.

Table 1. Matrix of characters of ingroup and two outgroups (bottom).

		1		2		3	
Taxon/character	12345	67890	12345	67890	12345	67890	1234
Benthobia atafona	10101	00121	10001	00011	21010	20101	1111
Benthobia complexirhyna	10101	00121	10001	00011	21010	20101	1111
Zemira australis	11010	01120	01111	10011	01121	11101	0111
Melapium lineatum	00100	13010	01111	11111	11121	21010	0011
Fulmentum ancilla	11110	00010	01101	11011	21111	11110	1111
Nassodonta dorri	10110	01011	00111	10111	?1110	2??01	0?11
Siratus senegalensis	00010	12000	01111	11111	11111	01110	0211
Conoidea	00100	00000	00001	00001	00010	00001	0011
Tonnoidea	00000	00000	00000	00000	00000	00000	0000

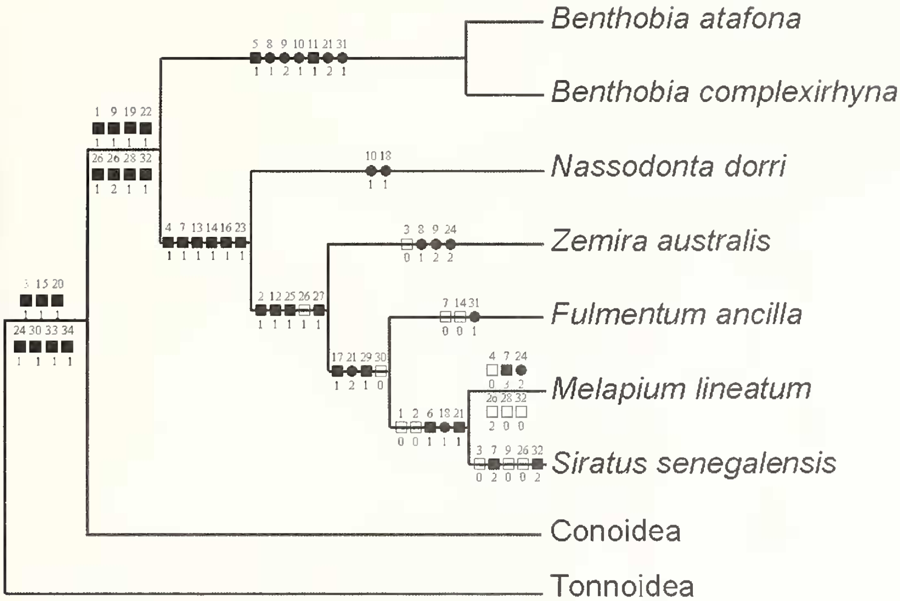

Figure 1. Single most parsimonious tree based on the data matrix in Table 1, with three outgroups operationally analyzed as part of the ingroup (Conoidea, *Siratus*, and *Nassodonta*). Length: 62; CI = 66; RI = 69. Each symbol indicates a synapomorphy supporting each node (only the homoplastic autapomorphies are shown) as follows: full square = non-homoplastic synapomorphy; circle = convergence; empty square = reversion.

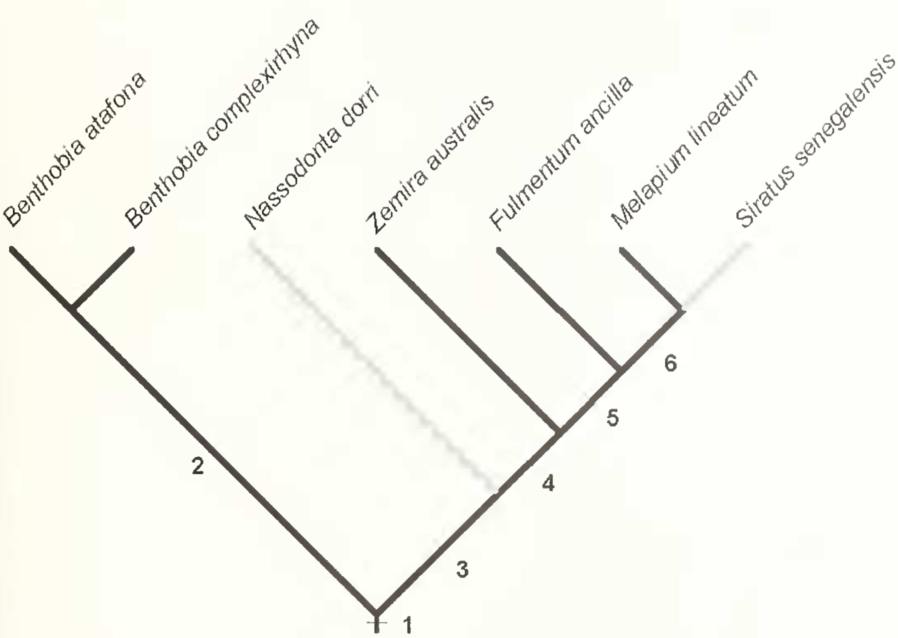

Figure 2. Single most parsimonious tree (same of Fig. 1, excluding both more basal outgroups) (Length: 62; CI = 66; RI = 69), with the nodes numbered. The gray branches represent the non-pseudolivid taxa, left branch a member of the Nassariidae, right branch a member of the Muricidae. The black branches represent the taxa mostly considered to be Pseudolividae, showing the polyphyletic nature of the taxon.

SYSTEMATICS

Genus *Zemira* Adams and Adams, 1853
(Type species *Eburna australis*, by monotypy)

Zemira australis (Sowerby, 1833)
(Figs. 3A-F, 4A-B, 5A-7H)

Synonymy: see Ponder and Darragh 1975: 101.
Complement:
Zemira australis: Ponder and Darragh 1975: 89-97, 101-104 (text figs. 1, 2, pl. 7 fig. 1-2. pl. 8 figs. 12-24); Smith 1998: 835-836 (fig. 15.165-C).

Description

Shell (Figs. 3A-C, 3F). Fusiform, pale brown, opaque. Protoconch, spherical, smooth, opaque, of about one whorl; boundary between protoconch and teleoconch unclear. Spire pointed, about half of length of body whorl. Suture well-marked by a subsutural, concave, wide groove, from protoconch up to outer lip; surface of groove smooth, external edge elevated, forming a low carina. Remaining regions sculptured by uniform, spiral, narrow furrows, about nine in penultimate whorl, about 10 in body whorl; one of these furrows, located between middle and anterior thirds of body whorl, deeper and wider (Figs. 3B-C). No umbilicus except a narrow furrow in inferior third around inner lip (Fig. 3A). Peristome oval, white, glossy (Figs. 3A, 3F). Canal short and narrow, left edge truncate, right edge wanting, as continuation of outer lip. Outer lip simple, cutting edge, rounded; very short tooth between middle and inferior thirds correspondent to deeper spiral furrow of body whorl (Figs. 3C, 3F); wide notch in superior region, at some distance from suture correspondent to sub-sutural carina. Inner lip simple, callus narrow, slightly more transparent than inner region of peristome.

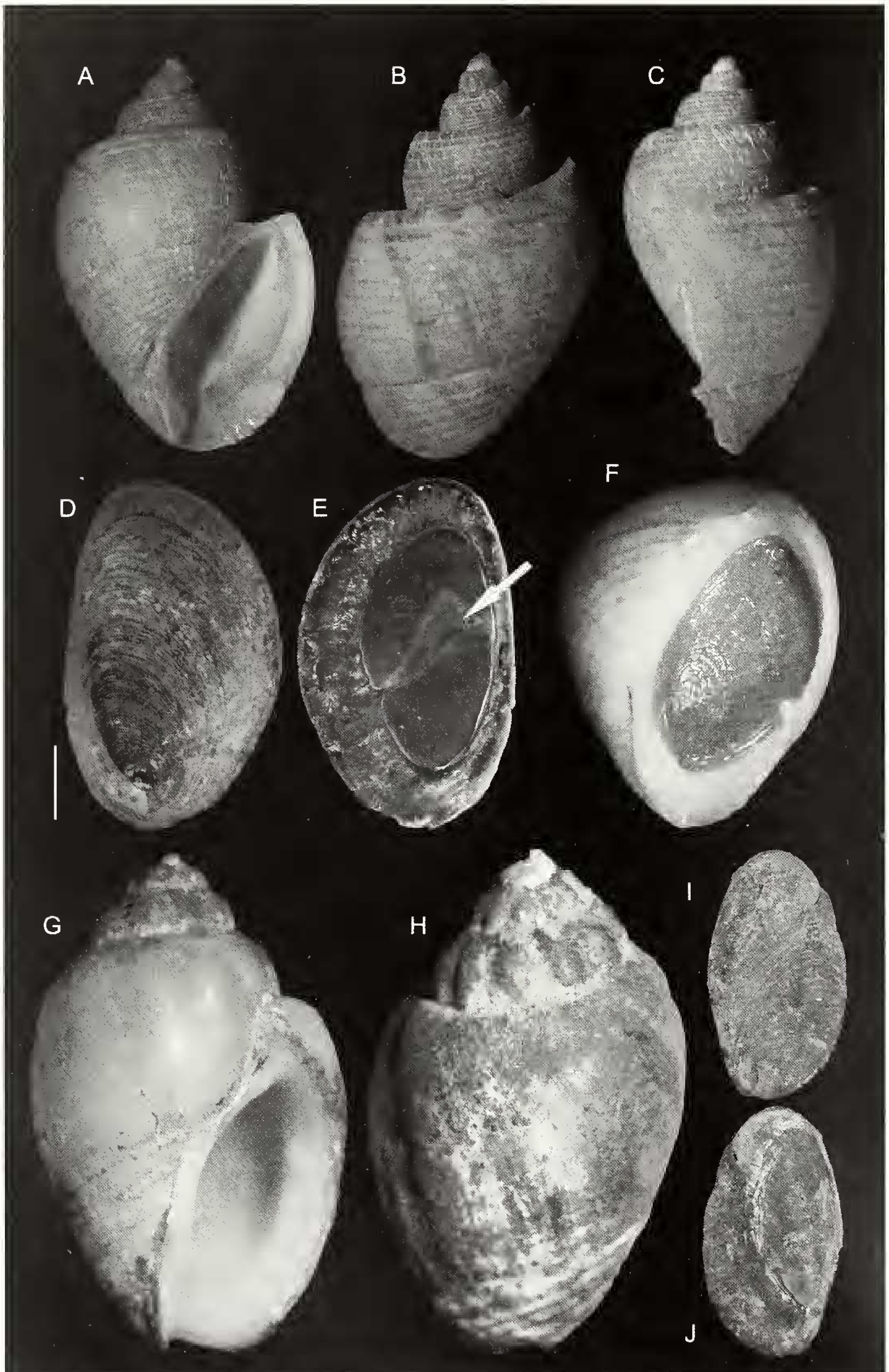

Figure 3. Shells and opercula. A-F, *Zemira australis*, AMS 333288. A-C, shell (specimen #1), female, apertural, dorsal and lateral views, length = 18.6 mm; D-E, operculum, outer and inner views, arrow indicates separation of two scar regions, scale bar = 2 mm; F, detail of aperture closed by operculum (specimen #4), showing labral tooth and opercular sculpture. G-J, *Nassodonta dorri*, MZSP 53533; G-H, shell, apertural and dorsal views, length = 13.6 mm; I-J, operculum, outer and inner views, length = 5 mm.

Head-foot (Figs. 5A, 5C, 5F). Head weakly protruded, bilobed, with single region pigmented by dark brown, the rest pale cream. Tentacles located close to each other and close to median line; tentacles' base very wide, flat, flap-like, outer edge rounded; distal half of tentacles marked by abrupt narrowing of the base, narrow, tapering gradually; tentacles' tip rounded. Foot broad, of about half whorl when retracted. Sole oval, edges thick and rounded. Anterior furrow of pedal glands deep, straight, thick superior and inferior edges, not reaching lateral-anterior end. Lateral region of the sole of the foot clearly extending beyond remaining dorsal regions of foot, division marked by a shallow longitudinal furrow lying somewhat in middle region between sole edge and dorsal region of foot (Fig. 5A). Opercular pad elliptical, almost as wide as the dorsal surface of the foot; possessing clear, median, oblique difference in levels (Fig. 5C); posterior half of this division forming small area with different, iridescent color. Columellar muscle thick, of about one half whorl. Male with large penis in posterior-right region behind the right tentacle described below.

Operculum (Figs. 3D-F). Elliptical, horny, pale to reddish brown. Nucleus sub-terminal, located closer to interior-inner edge. Outer surface with normal concentric growth lines, and series of radial lines produced by minute, aligned scales located on the growth lines, from nucleus to edges (Fig. 3F). Low carina running at some distance from inferior and inner edges, from nucleus up to middle level of inner edge. Inner surface glossy. Scar elliptical, occupying about 2/3 of inner area, somewhat dislocated closer to inner edge. Scar having two different levels of about the same area, one superior and another inferior; both separated by a wide chevron, marking a low step (Fig. 3E, arrow); a small notch in region where the chevron touches outer scar edge.

Mantle organs (Figs. 5B, 5D). Mantle edge simple, thick. Siphon small, not extending beyond mantle edge. Osphradium about 1/3 the width of the pallial cavity and ¾ of its length. Osphradium filaments tall, central region scalloped by 5 folds in the left and 6 folds in the right filaments (Fig. 5B: os). Osphradium filaments widely attached along mantle roof. Osphradium anterior end curved to the left, with left filaments clearly smaller than right filaments; remaining osphradial regions with somewhat symmetrical filaments (left filaments slightly smaller). Very narrow area between osphradium and gill. Ctenidial vein narrow, dislocated weakly beyond left gill edge, towards right edge of osphradium. Gill slightly longer than the osphradium and of about the same width; its anterior end broadly pointed, located closer to the mantle edge, far from anterior end of osphradium; posterior gill end located slightly posterior to that of osphradium. Afferent gill vessel very narrow, lying at a short distance from the right edge of the gill. Between the gill and the right edge of pallial cavity there is an area equivalent in width to that of the gill. The hypobranchial gland is thin, greenish beige, covering most of the area between the gill and the rectum, including the left and ventral surfaces of the rectum; the anterior region of the hypobranchial gland tapers gradually. Rectum narrow, running along the right edge of the pallial cavity (Figs. 5B, 5D-E). Anus simple, sessile, located between middle and anterior thirds of pallial cavity. Pallial gonoducts located between rectum and pallial floor, described below.

Visceral mass (Fig. 5D). Anterior whorl mostly occupied by stomach, kidney, and pericardium (Figs. 5E, 6E). Digestive gland greenish brown, located along inferior region of each visceral whorl, covering middle digestive tubes and also two whorls poste-

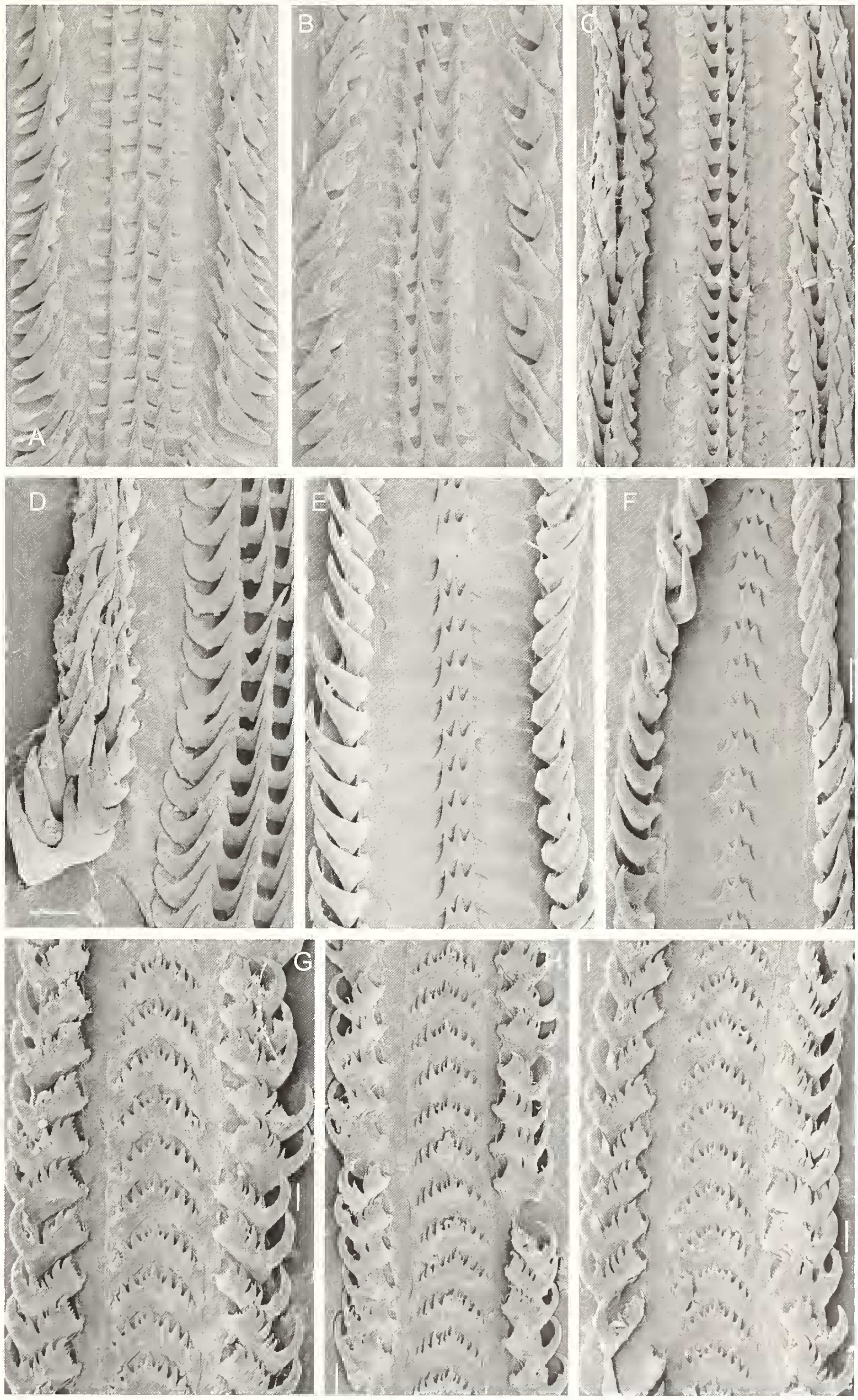

Figure 4. Scanning electron micrographs of radulae. A-B, *Zemira australis*, scale bars = 30 µm. C-D, *Fulmentum ancilla*, scale bars = 50 µm. E-F, *Melapium lineatum*, scale bars = 50 µm. G-I, *Nassodonta dorri*, scale bars = 30 µm.

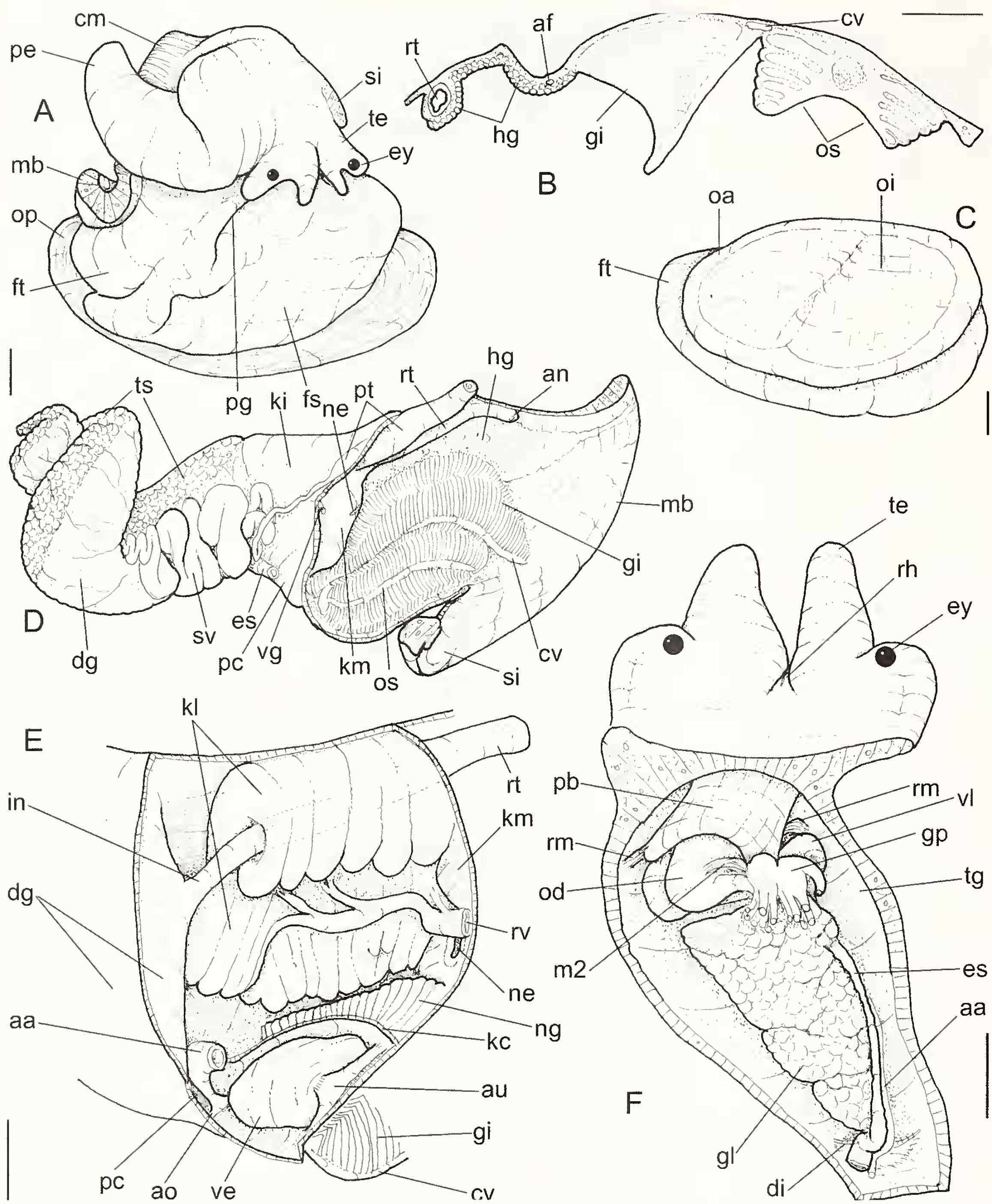

Figure 5. *Zemira australis* anatomy. A, head-foot, male, frontal view. B, pallial cavity roof, transverse section at middle level of osphradium. C, foot, detail of opercular pad, dorsal view, operculum removed. D, pallial cavity, ventral-inner view, and visceral mass, male. E, region of kidney, ventral view, ventral wall of kidney and pericardium removed, anterior membrane partially deflected to right. F, head and haemocoel, ventral view, foot removed. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

rior to stomach. Gonad pale beige, lying along superior and columellar surfaces of visceral whorls posterior to stomach.

Circulatory and excretory systems (Fig. 5E). Pericardium located just posterior to gill, along the left anterior region of the visceral mass (Fig. 5D). Auricle small, triangular, attached to anterior surface of pericardium, with the ctenidial vein entering from the left and the connection to kidney at its right end. Auricle connected to anterior surface of ventricle. Ventricle very large, filling most of pericardium volume. Aortas located along posterior region of the ventricle; anterior aorta about 4 times larger than posterior aorta, and located ventral to it. Kidney occupies about 1/3 of pallial cavity volume, located along middle and right regions of the anterior end of the visceral mass. Nephridial gland triangular in section, broader anteriorly, gradually narrowing posteriorly; lying along the dorsal region of the renopericardial wall. Renal lobe occupying most of the kidney's interior volume, presenting two flaps of similar thickness, fused along right region; ventral flap shorter (about half of dorsal flap), intestine running through it; dorsal flap occupying most of renal dorsal surface. Afferent renal vessel large, running from the haemocoel, covering right side of nephropore, with some branches inserted in inner surface of dorsal flap of renal lobe.

Digestive system (Figs. 5F-8A). **Proboscis** relatively short (about 1/3 of haemocoel length) (Figs. 5F, 7A: pb). Mouth transverse along proboscis tip. Buccal cavity with pair of broad and tall lateral folds, each one dividing within a short distance, one branch running to the odontophore tube, the other to the esophagus (Fig. 5F). Ventral surface between buccal folds with a clear, low, flat, chitinous platform (Fig. 7F: ol). Odontophore oval, about half the length of the proboscis (Figs. 7A, 7E). Odontophore tube connecting it with buccal cavity. **Odontophore** muscles (Figs. 6A-D, 7E-F): **m1**, several small muscle fibers connecting buccal mass to adjacent inner surface of proboscis; **mj**, pair of peribuccal muscles and protractor of odontophore, origin thin within dorsal wall of oral cavity, running along odontophore tube becoming thicker, inserting into outer surface of cartilages, externally to m6 and medially to m4, in two branches, one anterior and another posterior, posterior branch about twice the size of and longer than the anterior branch; **m2**, pair of retractor muscles of odontophore, originating in ventral surface of haemocoel, in region just posterior to proboscis (when retracted), running dorsally, with median fibers running through nerve ring, inserting into posterior surface of odontophore, part into m5 and part into m4 regions close to median line; **m2a**, auxiliary of m2, being single and running between both m2, attached to ventral surface of anterior aorta; its fibers apparently originated ventral to nerve ring, not passing through it (Figs. 6A-D); **m3**, pair of thin dorsal protractor muscles of odontophore, originating in anterior-dorsal end of odontophore tube, at its juncture with the esophagus, running posteriorly, covering dorsal surface of odontophore tube, inserting into odontophore middle-dorsal surface (Figs. 7E-F); **m4**, strong pair of dorsal tensor radular muscles, originating in odontophore cartilages along a line surrounding their ventral surface, running towards dorsal surrounding lateral surface of cartilages, inserting laterally along radular sac into the region near the buccal cavity; **m5**, pair of secondary dorsal tensor muscles of radula, originating in posterior and medial regions of the cartilages, running dorsal and medial as continuation from m4, inserting into radular sac near the buccal cavity alongside and medial to m4 insertion; **m6**, thin horizontal muscle, uniting both odontophore cartilages, with about 3/4 of cartilage length, inserting along a line into the ventral and external surfaces of the cartilages, at a short distance from their inner-ventral edge, starting at the anterior end of the cartilages and ending just before their posterior quarter (Figs. 6B-C); **m11a**, pair of ventral tensor muscles of radula, thin, somewhat broad, originating partly in the posterior-ventral end of cartilages and partly in the m2 insertion, running anteriorly covering m6, inserting into ventral edge of radula and subradular cartilage, and some inner portion preceding this (Fig. 6D); **m14**, pair of ventral protractor muscles of odontophore, originating along ventral surface of oral tube and tube of odontophore, running posteriorly at short distance from median line, covering central surface of odontophore, inserting into posterior-ventral surface of odontophore, close to m2 insertion (Fig. 7E). Other non-muscular odontophore structures: **sc**, subradular cartilage, expanding in exposed region of radula into buccal cavity, covering neighboring surface of radula (Figs. 6A, 6D, 7F); **oc**, odontophore cartilages, somewhat elliptical, flat, with medial-ventral edge slightly straighter than outer edge, posterior region clearly narrow (Figs. 6B, 6C); **br**, subradular membrane, covering inner surface of subradular cartilage and radula, m4, m5, and m11a insertions. **Radula** (Figs. 4A-B): **rachidian** tooth with short transverse base, spanning about 1/3 of radular ribbon, 3 long, tall (about 2/3 of base length), sharp pointed cusps somewhat equidistant from each other, central cusp symmetrical, outer cusps weakly turned outwardly; between rachidian and lateral teeth a distance equivalent to 1/3 of rachidian width; **lateral tooth** hook-like, base broad (equivalent to 2/3 of rachidian base width), gradually narrowing up to sharply pointed tip, height about 1.5 that of rachidian; straight to weakly curved inwardly. **Salivary glands** clustering along anterior region of valve of Leiblein and ventral ganglia of nerve ring, attaching to lateral surface of the anterior esophagus just anterior to the valve of Leiblein (Figs. 7A-B); their ducts very narrow, totally at-

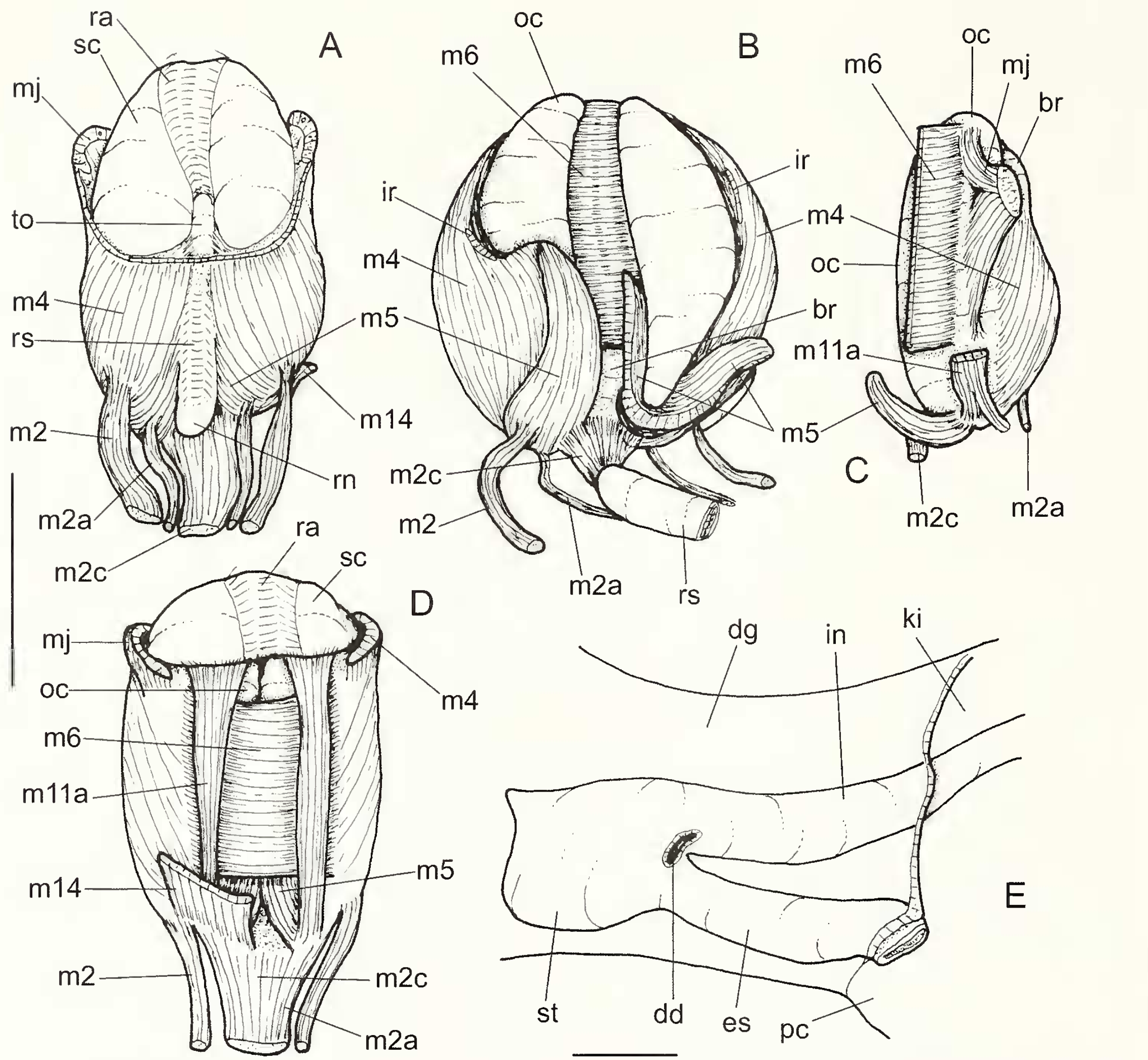

Figure 6. *Zemira australis* anatomy. A, odontophore, dorsal view, anterior odontophore tube removed. B, same, outer layer of muscles and radular apparatus removed and only partially shown (rs). C, odontophore, ventral view, only its right side shown, posterior muscles deflected. D, same, outer view, outer layer of muscles and membrane partially removed. E, midgut, ventral view as *in situ*, some adjacent structures also shown. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

tached to anterior esophagus wall and to lateral wall of oral tube; opening very small (Fig. 7F: sa), into anterior region of lateral folds of buccal cavity, somewhat ventrally, just within the anterior end of a narrow furrow surrounding the ventral edge of the odontophore tube folds. **Anterior esophagus** with somewhat thick walls, length equivalent to that of odontophore, inner surface with lateral, longitudinal, low, and flat folds that become narrower posteriorly. Between these folds are secondary, low, narrow folds (Fig. 7F). **Valve of Leiblein** with about 1/4 of odontophore volume, anterior region with a transverse, white band into which long cilia insert, middle and posterior regions pale beige, corresponding to a tall inner gland occupying most of inner surface; oblique furrow (by pass) present, separating all valve regions (Figs. 7A-B); inner surface smooth, not glandular, bordered by pair of low and very narrow folds that diverge in its anterior region, and continuous with middle esophagus folds posteriorly. **Middle esophagus** about half as long as

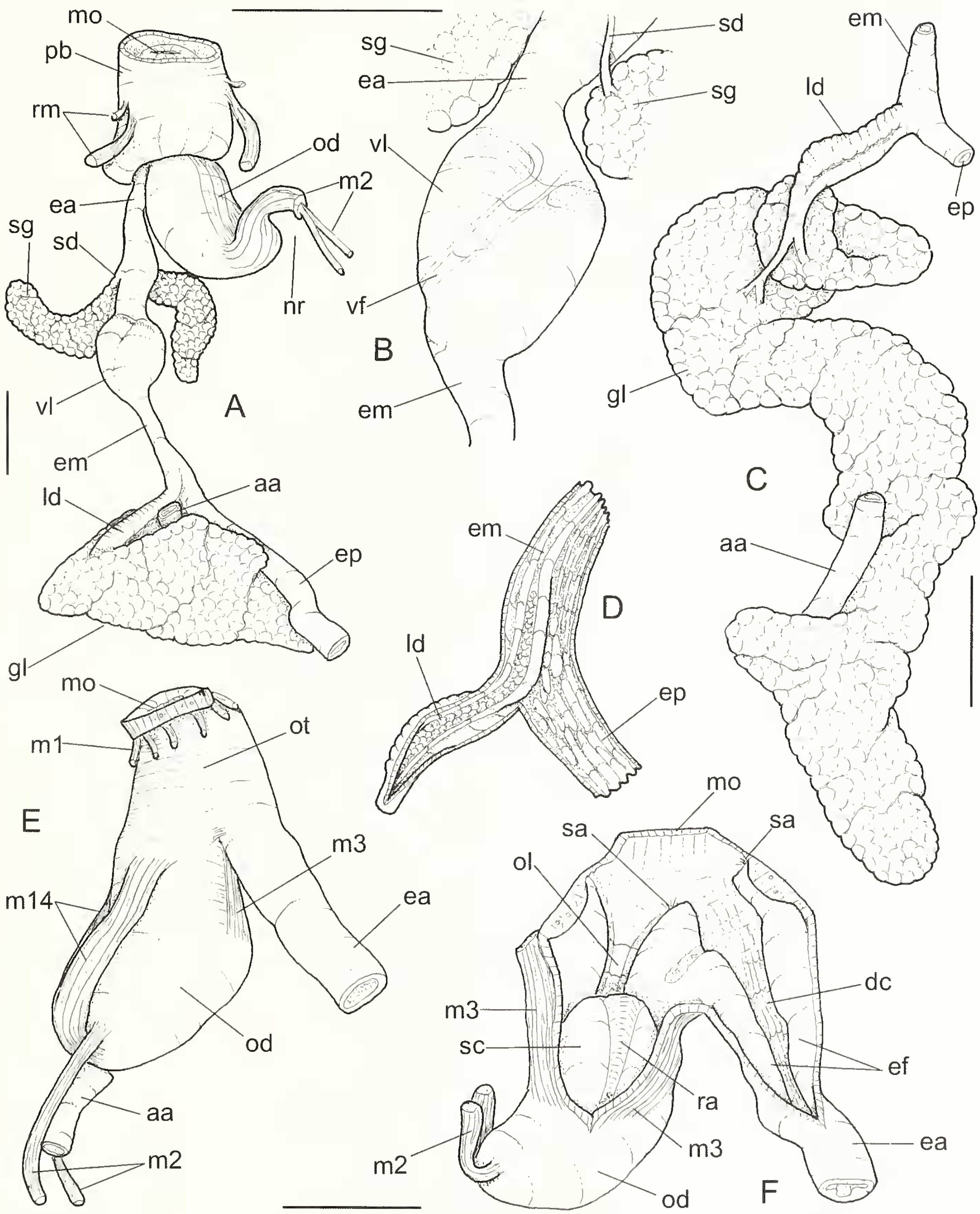

Figure 7. *Zemira australis* anatomy. A, foregut, extended, ventral view. B, region of the valve of Leiblein, its oblique furrow (vf) seen by transparency. C, gland of Leiblein partially uncoiled, some adjacent structures also shown. D, transition between middle and posterior esophagus and duct of gland of Leiblein, opened longitudinally to expose inner folds. E, buccal mass, left view. F, buccal mass, anterior region opened longitudinally and deflected to expose inner surfaces. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

anterior esophagus (Fig. 7A: em), walls thin; inner surface with longitudinal, low, narrow folds, a pair of close folds larger (Fig. 7D), running towards duct of gland of Leiblein. **Gland of Leiblein** triangular *in situ* (Figs. 5F, 7A), long and somewhat flat if uncoiled (Fig. 7C), becoming about as long as posterior esophagus; anterior aorta crossing between middle and posterior thirds of this gland. Duct of gland of Leiblein long and narrow (about as long as middle esophagus, and about half of its diameter) (Figs. 7A, 7D); having two origins, one sub-terminal in anterior end of the gland, the other in a portion more posterior (Fig. 7C); these two ducts unite within a short distance, remaining duct having pair of tall, longitudinal, narrow folds (continuation from larger folds of middle esophagus); these folds separate a narrow, white, multi-lobed secondary gland from a smooth, narrow area; this secondary gland occupies about 2/3 of duct volume, ending abruptly before the duct's insertion into the esophagus (Fig. 7D). **Posterior esophagus** (Figs. 7A, 7D: ep) about twice as long as the anterior esophagus, inner surface with narrow longitudinal folds, some low, others taller (covering lower folds) diverging and coalescing randomly; these folds disappearing abruptly before stomach. **Stomach** spherical, blind sac, about half the width of adjacent visceral whorl. Esophagus enters stomach along its left anterior region (Figs. 6E, 8A: st), intestine originates to the right of the esophageal insertion. Gastric inner surface (Fig. 8A) mostly smooth, except for a pair of low, narrow folds that run along its left surface, from the esophageal insertion, disappearing gradually into the posterior gastric surface. Duct to digestive gland single, wide, located between esophageal insertion and intestinal origin (Fig. 6E). **Intestine** with tall, dorsal, smooth, long and triangular platform adjacent to the stomach (Fig. 8A); left edge of this platform alongside a band of longitudinal, narrow folds; right edge of this platform serving as insertion of several transversal folds, each about twice as wide as the longitudinal folds, becoming gradually oblique, surrounding ventral surface of intestine, ending at left edge of band with longitudinal folds. Inner surface of intestine, beyond this platform, with only longitudinal folds, very close to each other, filling inner surface totally. Intestine runs almost straight anteriorly, crossing through anterior region of digestive gland, kidney lobe, and right edge of pallial cavity (Figs. 5E, 6E). Rectum and anus described above (pallial cavity).

Genital system. Male (Figs. 5A, 8B). Visceral vas deferens begins a half whorl before anterior end of testis. Within a short distance it becomes a very broad, intensely coiled seminal vesicle, occupying about half of adjacent visceral whorl (Fig. 5D). Seminal vesicle located in the ventral surface of last whorl of the visceral mass, posterior to kidney; becomes narrow at some distance posterior from pallial cavity, running about 1/6 whorl. Prostate gland relatively narrow, running along right edge of pallial cavity ventral to rectum, visceral vas deferens inserting posteriorly (Fig. 5D: pt); walls thick-glandular; no apertures to pallial cavity; inner lumen surrounded by muscle fibers. Prostate spans about ⅓ pallial cavity length, gradually becoming narrow, crossing to pallial floor. This region in the pallial cavity floor with thick, muscular walls, slightly convolute up to penis base (Fig. 8B). Penis slightly larger than half of pallial cavity volume, stubby, dorso-ventrally flat (Figs. 5A, 8B); base broad, with a large, broad right fold covering base of right tentacle; then twisting, remaining tall, flat and thick, narrowing gradually up to bluntly pointed tip (Fig. 8B). Pallial vas deferens within the integument, becoming penis duct. Penis duct running approximately along penis center, very narrow, weakly coiled. Penis aperture apical, very small.

Female (Figs. 8C-F). Visceral oviduct very narrow, running along middle region of columellar surface of the last whorl of the visceral mass, about ¼ whorl preceding pallial cavity, gradually becoming thicker, inserting into pallial oviduct without clear separation. Posterior region of pallial oviduct protruding into kidney, having a narrow zigzag. Albumen (whitish) and capsule (beige) glands adjacent, albumen gland spanning posterior 1/5 of pallial oviduct. Seminal receptacle very small, located between albumen and capsule glands (Fig. 8C); flat to rounded; duct very narrow, attached along the dorsal surface of the pallial oviduct, opening into the vaginal furrow between the albumen and capsule glands. Capsule gland with flat lumen, vaginal furrow running along its left edge, with surface smooth (Fig. 8D). Female pore wide, protruded, with thick edges (Figs. 8E-F: fp). Bursa copulatrix small, short, located along left side of the distal, detached portion of the pallial oviduct (Fig. 8F: bc); with thick muscular walls; its aperture turned anteriorly, occupying about 2/3 of total female pore; inner surface with low, wide, longitudinal folds. Capsule gland aperture narrow, situated to the right of the bursa aperture; its walls thick muscular, protruding inside the chamber of the terminal atrium of the capsule gland. Terminal atrium, with thin walls, located between capsule gland anterior and female pore. Female pore with several wide, longitudinal folds. No cement gland in foot sole.

Central nervous system (Figs. 8G-H). Relatively well-concentrated. No distinction between pleural and cerebral ganglia. Cerebral ganglia broadly connected to each other. Pedal ganglia slightly smaller than cerebro-pleural ganglia; pedal commissure broad, but narrower than cerebral commissure. Cerebro-pedal and pleuro-pedal connectives short, but distinguishable. Pair of buccal ganglia small, located close to posterior edge of the cerebral ganglia.

Measurements of shells (in mm). AMS C333288: ♀1 = 18.6 by 12.0; ♂2 = 19.3 by 12.2; ♂3 = 16.6 by 9.8; ♀4 = 14.1 by 8.7.

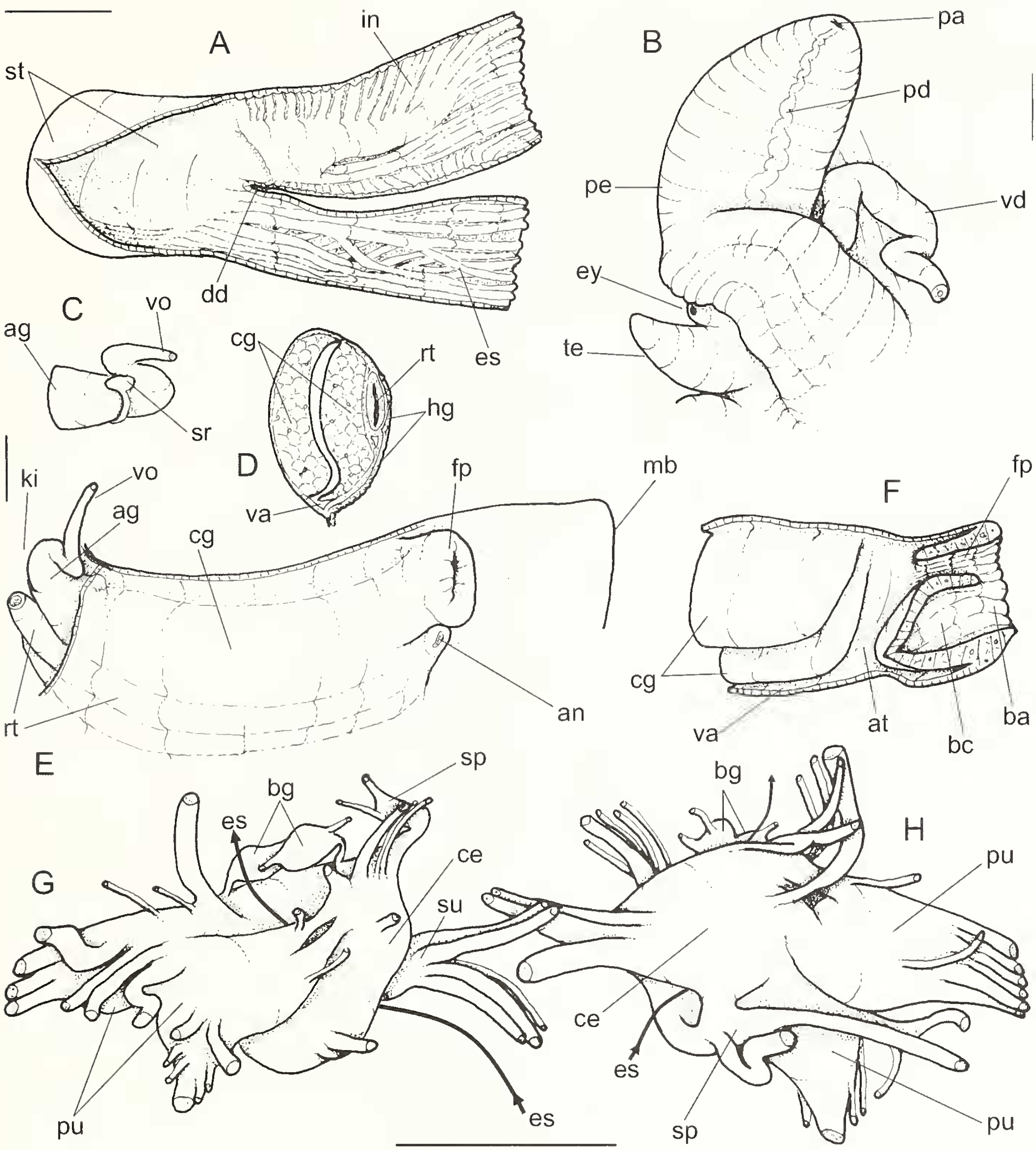

Figure 8. *Zemira australis* anatomy. A, stomach, ventral view, its ventral wall and adjacent region of intestine (in) and esophagus (es) opened longitudinally, inner surface exposed. B, penis and adjacent region of its base, ventral view, penis partially deflected, its duct (pd) seen by transparency. C, pallial oviduct, dorsal view, detail of its posterior region. D, pallial oviduct, transversal section though its middle region. E, pallial oviduct, entire ventral view, including its portion in kidney chamber. F, same, detail of its anterior end, ventral wall removed, region of pore opened longitudinally and deflected to show its parts. G, central nervous system, ventral, slightly right oblique view, esophageal passage (es) shown by arrow. H, same, dorsal, slightly left oblique view. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

Distribution. East coast of Australia.

Habitat. Sandy, from 3 to 146 m depth (Beechey 2005).

Material examined. AUSTRALIA. **New South Wales**; Sydney (Shelf Benthic Survey col.), 1.6 km east of Malabar outlet, 33°58.250′S 151°17.000′E, 66 m depth, AMS C092091, 3♀ (Sta. 027653, SBS3, 26/iii/1973), 2.3 km east of Malabar outlet, 33°59.450′S 151°16.800′E, 66 m depth, AMS C333288, 3♂, 6♀ (Sta. 002609E, SBS5, 25/x/1973), 2.6 km east of Cape Banks, 33°59.500′S 151°16.740′E, 66 m depth, AMS C406792, 1♂ (Sta. 038772, SBS25, 26/i/1973).

Genus *Fulmentum* Fischer, 1884
(Type species *Buccinum sepimentum* Rang, 1832, by monotypy)

Fulmentum ancilla (Hanley, 1859)
(Figs. 9A-E, 4C-D, 10A-13F)

Pseudoliva ancilla: Kantor 1991: 31-34 (figs. 12, 13); Hayes 1994: 77-78.
Sylvanocochlis ancilla: Lorenz 1989: 16-18.
Fulmentum ancilla: Vermeij 1998: 60.

Description

Shell (Figs. 9A-B, 9E). Large (about 60 mm), heavy, biconical. Color brown to beige. Periostracum velvet-like, rust colored, partially eroded. Spire conical, aperture spanning 70% of shell length. Protoconch of 1½ whorls, white, smooth, to weakly reticulated in some areas, border with teleoconch unclear. Teleoconch of 5-6 whorls, each whorl with a weakly concave shoulder. Axial sculpture limited to growth lines. A wide spiral furrow runs along the anterior third of the shell, forming a low, broad labral tooth. Umbilicus absent. Aperture elliptical, posterior end pointed. Siphonal canal wide, open, very short. Inner lip smooth, callus narrow and low except for a small, low node at some distance from posterior end. Outer lip with simple edge, thickened at the shoulder and in region of the labral spine. Thickening of the outer lip and the callus of the inner lip located just posterior to the spiral furrow on the previous whorl.

Head-foot (Figs. 9E, 10B-C, 11A). Head not protruded. Color mostly pale beige, with dark brown, coalescent (forming wide transversal bands) spots in head and dorsal surface of foot (Fig. 9E). Tentacles relatively short, located close to each other; basal half clearly thicker than distal half. Eyes located along outer edge of tentacles at middle level, proximal to their constriction; terminal portion of tentacle very short (Figs. 10B-C). Rhynchostome located ventral to and between the tentacles. Foot spans ½ whorl when retracted; sole simple; anterior edge with deep furrow that contains the pedal glands. Dorsal and ventral edges of this furrow relatively thick and rounded; both ends of anterior edge rounded. Columellar muscle spans ½ whorl, thick; posterior end with a wide, rounded component, and a small (about 10% of origin area) projection located along its left end. Haemocoel about 1/3 head-foot width along its anterior half, posterior half becomes very narrow and turned to the left (Fig. 10C).

Operculum (Figs. 9C-D). Elliptical, horny, brown, occupying entire shell aperture. Nucleus terminal, inferior. Outer surface with concentric growth lines and narrow undulations. Inner surface glossy. Scar occupying about 80% of inner surface, approx. central, slightly displaced closer to inner and superior edges. Scar divided into approx. two similar sized areas by oblique line. Inferior region broadly pointed, with wide free projection; triangular, wide furrow running along middle region of this projection, starting in the apex, finishing in the scar.

Mantle organs (Figs. 10A, 10E). Mantle edge simple, thick, transversally banded. Siphon relatively long (about half of pallial cavity length), edges simple (Figs. 9E, 10A); mantle edge surrounding its base. Pallial cavity with about 1½ whorls. Osphradium about ½ pallial cavity length and about ¼ of its width, with curved, symmetrical filaments; anterior and posterior ends rounded; each filament relatively tall, projecting laterally; dorsal edge connected to mantle along ½ its length the rest supported by a rod; ventral edge thin, with small notch located approximately in central region; right filaments covering ctenidial vein and part of gill filament bases (Fig. 10E: os). Gill about 3/4 of pallial cavity length and 1/4 of its width; anterior end pointed, posterior to that of osphradium; ctenidial vein extending a short distance anterior to gill end; posterior gill end rounded, touching pericardium. Gill filaments triangular and tall, curved to right; rod relatively broad; filament tip rounded, preceded by narrow region. Ctenidial vein narrow, lying along left edge of gill. Afferent gill vessel very narrow, lying at some distance from apparent right gill edge. Hypobranchial gland somewhat tall, whitish, covering entire area between gill and rectum (about ½ pallial cavity width), anterior end at level of anus. Rectum relatively narrow, running along right edge of pallial cavity. Anus detached, situated between middle and anterior thirds of pallial cavity, with small papilla on its right side. Genital ducts lying between rectum and right edge of cavity, described below.

Visceral mass (Fig. 10A). Spans about three whorls. Reno-pericardial structures occupy anterior half whorl. Stomach located just posterior to reno-pericardial area. Digestive gland greenish cream, occupying all whorls, surrounding stomach. Gonad same color as digestive gland, occupying superior and columellar surface of each visceral whorl, terminating a short distance posterior to kidney.

Circulatory and excretory systems (Fig. 10D). Pericardium about ¼ of kidney volume. Heart similar to that of *Zemira*. Kidney somewhat trapezoid, spanning ~½ half whorl. Nephridial gland flat, thicker anteriorly, lying along entire dorsal half of reno-pericardial membrane. Kidney lobe similar to that of *Zemira*. Afferent renal vessel large, with branches running between folds of both kidney lobe flaps, covering right side of nephropore, connected to membrane between kidney and pallial cavities, producing small urinary cavity.

Digestive system (Figs. 11A-12E). Rhynchostome forms a small opening located ventral to and between both cephalic

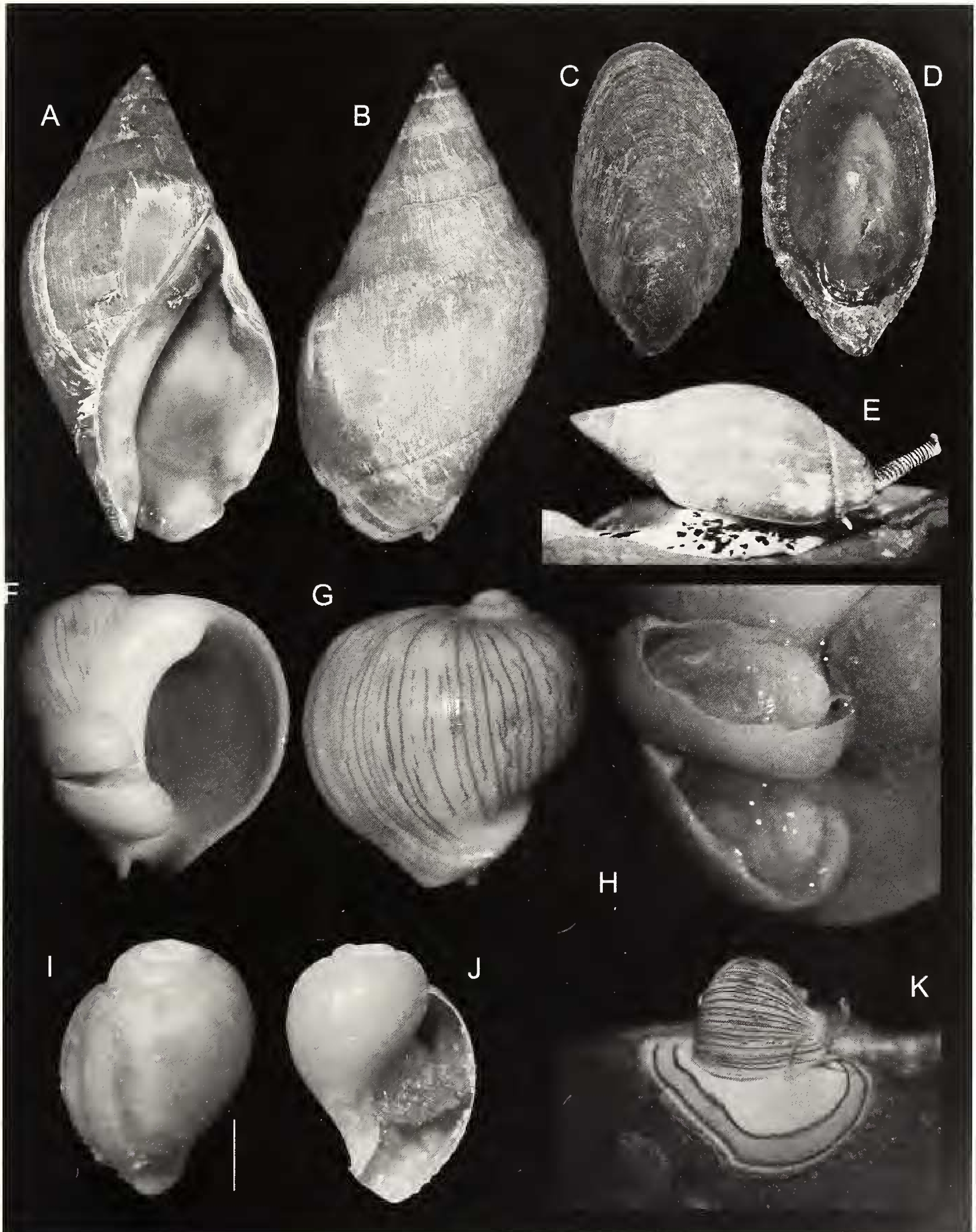

Figure 9. Shells, opercula, and living specimens. A-E, *Fulmentum ancilla*; A-B, shell, NMNH E5279, female, apertural and dorsal views, length = 64.5 mm. C-D, Operculum, outer and inner views. E, Live, crawling specimen from Jeffreys Bay, South Africa, photo courtesy of Brian Hayes. F-K, *Melapium lineatum*. F-G, shell, NMNH V9979, male, apertural and dorsal views, 2 egg capsules attached in anterior region of inner lip (total length = 26,2 mm). H, detail of egg capsules attached to shell, NMNH 59733, portions of both capsules removed, showing young specimens inside. I-J, dorsal and apertural views of a young specimen extracted from an egg capsule shown in the preceding figure, scale bar = 2 mm. K, live, crawling specimen from off Algoa Bay, South Africa, photo courtesy of Brian Hayes.

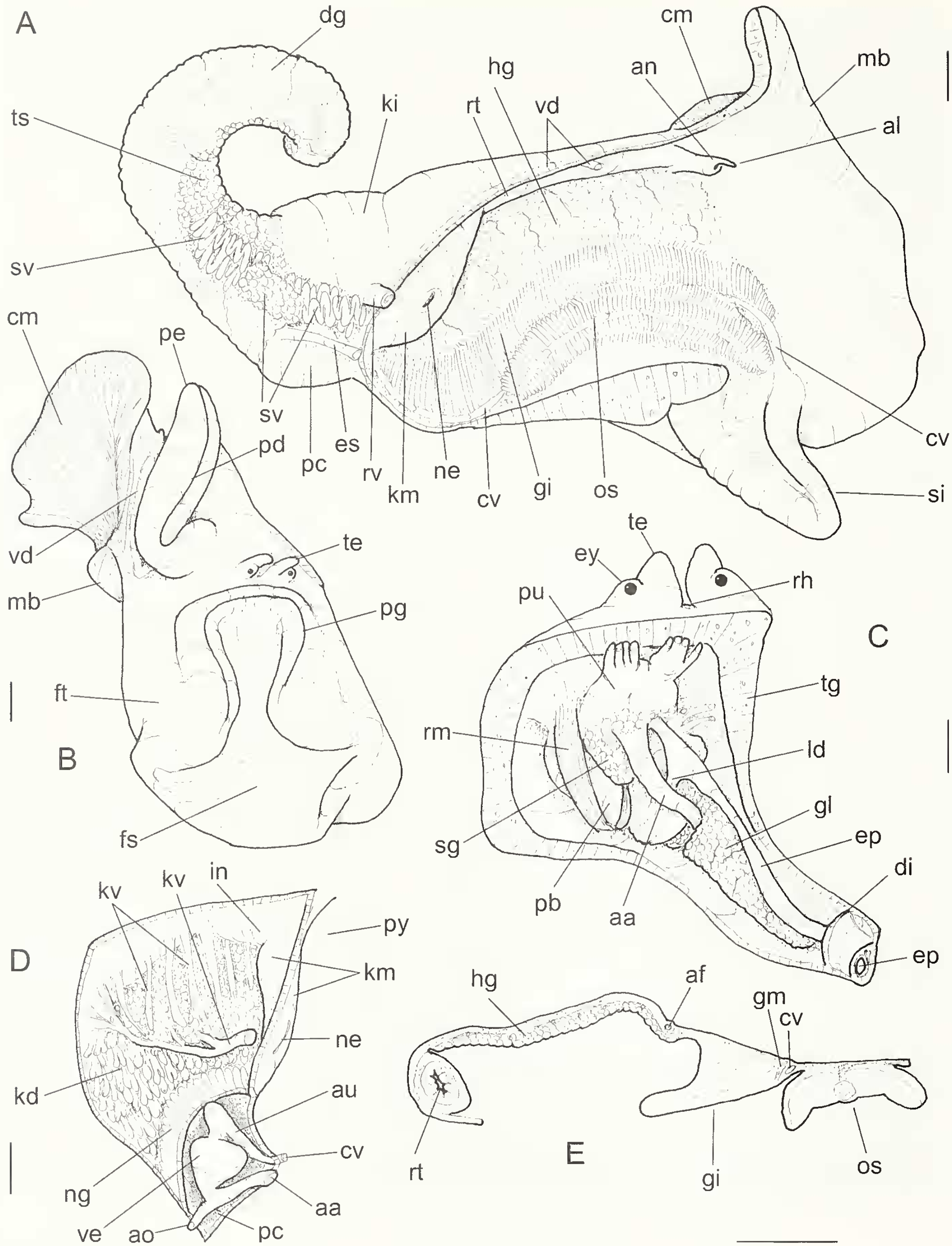

Figure 10. *Fulmentum ancilla* anatomy. A, pallial cavity and visceral mass, male, ventral-inner view. B, head-foot, male, frontal view. C, head and haemocoel, ventral view, foot and columellar muscle removed. D, kidney and pericardium, ventral view, ventral wall removed, renal membrane with pallial cavity (km) deflected anteriorly (right in fig.). E, Transverse section through pallial cavity roof, at mid-length of the osphradium. Scale bars = 2 mm. Abbreviations listed in section with figure captions.

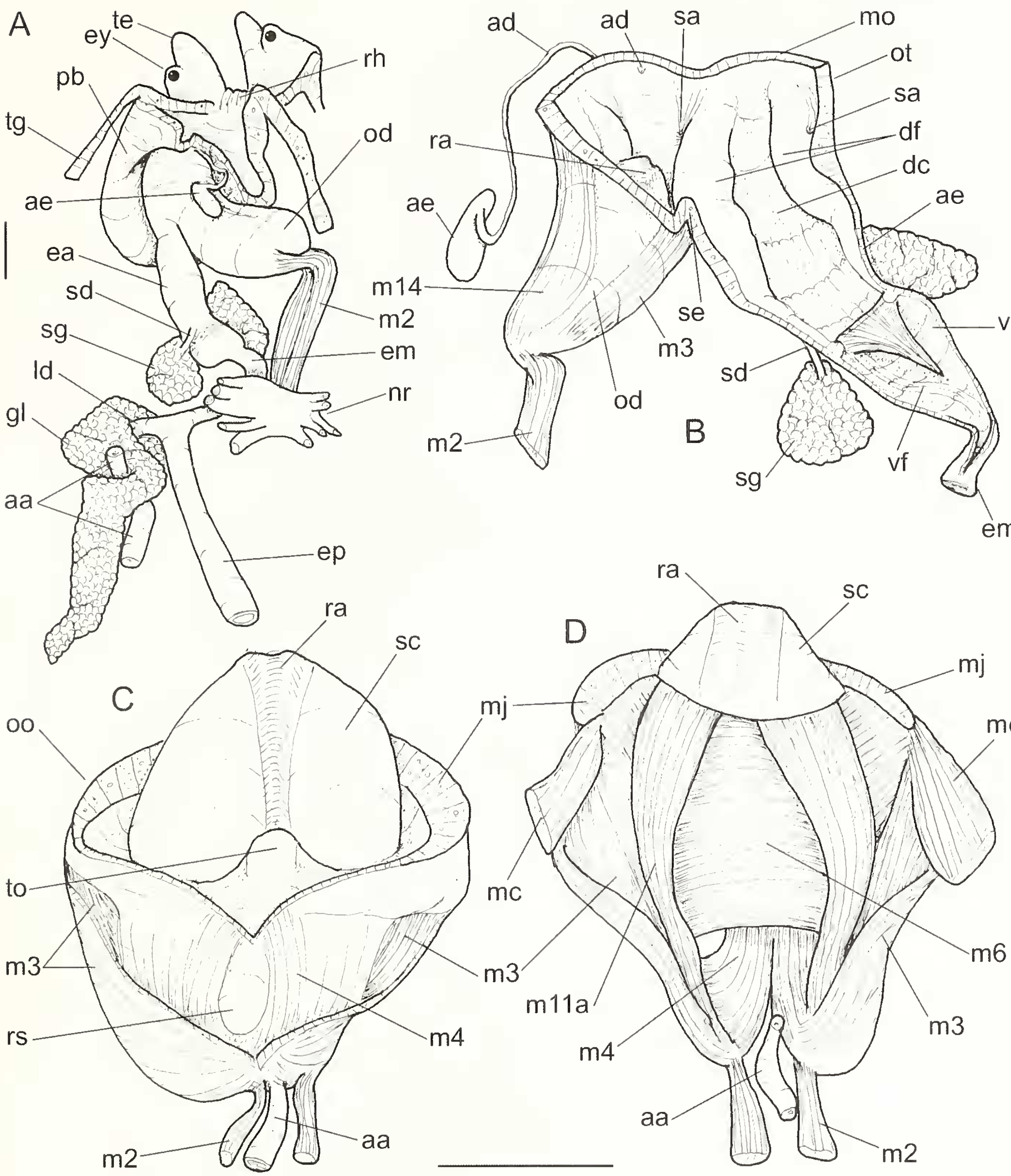

Figure 11. *Fulmentum ancilla* anatomy. A, foregut partially uncoiled, ventral view, adjacent region of head also shown. B, buccal mass, left view, esophagus opened longitudinally. C, odontophore, dorsal view, some muscles deflected. D, same, dorsal view, superficial layers of muscles and membrane reflected, aorta shown as *in situ*. Scale bars = 2 mm. Abbreviations listed in section with figure captions.

tentacles (Fig. 10C). **Proboscis** short (less than 1/3 of haemocoel length) and broad (about haemocoel width) (Figs. 10C, 11A); walls thick, muscular. Proboscis retractor muscles forming a main pair, one in each side, left retractor muscle slightly more dorsal than right, originating at middle level of haemocoel latero-ventral region, running towards middle level of proboscis, inserting along its distal half (Fig. 10C: rm); several accessory proboscis retractor muscles along dorsal surface, thinner than main retractor muscles, originating in a virtual line connecting both main retractor muscles, surrounding dorsal haemocoelic wall. Mouth a transversal slit on proboscis tip. Oral tube with thick walls, about half the length of the odontophore. Oral cavity wide, with a pair of low, broad, dorsal folds, each occupying about 1/3 of the dorsal surface and 1/3 of area between them; each dorsal fold with rounded anterior end, at short distance from mouth (Fig. 11B); remaining fold characters similar to those of *Zemira*. Ventral chitinous platform present (Fig. 11B, ad). Odontophore about same length as proboscis (when extended), protruding beyond proboscis into haemocoel when retracted (Figs. 10C, 11A). Odontophore organization and musculature similar to that of *Zemira*, with following distinctions. Odontophore muscles (Figs. 11B-12A): **m2** a single pair inserted into posterior region of m4, by side of radular sac; **m2a** absent; **m5** pair wider and thicker; **m6** with anterior end at some distance from that of odontophore cartilages (Fig. 10); **m11a** pair broader (Fig. 11D). Odontophore cartilages elliptical, with posterior region similar to anterior region (Fig. 12A). **Radula** (Figs. 4C-D): **rachidian** tooth with broad base (about 60% of radular ribbon), close to adjacent teeth, with 3 tall (about 1/2 base width), triangular, sharply pointed cusps, somewhat equidistant and separated from each other; distance between rachidian and lateral teeth area equivalent to half of rachidian base width; **lateral tooth** with base 60% of rachidian width, 2 tall (height equivalent to base width), triangular, sharply pointed cusps, one on each side of the tooth, inner cusp slightly smaller than outer cusp. **Anterior esophagus** shorter than odontophore, wall thick muscular, with some muscles connecting its latero-ventral region to the adjacent region of the haemocoel floor, sometimes passing through the salivary glands; inner surface with a pair of lateral folds, as continuations from buccal cavity folds, gradually narrowing (Figs. 11A-B: ae). **Salivary glands** paired, each an elliptical, separated mass located along each side of valve of Leiblein and close to the nerve ring (Figs. 11A-B, 12B: sg). Salivary ducts very narrow, originating in the anterior end of the gland, penetrating the lateral walls of the anterior esophagus within a very short distance; running within this wall up to salivary aperture. Salivary aperture very small, located in lateral edge of buccal cavity dorsal folds, at mid-level, just within the posterior end of a narrow and shallow furrow running anteriorly, surrounding antero-lateral edge of dorsal folds (Fig. 11B: sa). **Accessory salivary gland** single, elliptical, internally hollow, situated within the haemocoel near the middle region of odontophore's ventral surface. Anterior region of gland gradually narrowing without clear division from its duct. Duct long and very narrow, equal to the length of odontophore, lying along ventral surface of the odontophore, odontophore tube and oral tube (Figs. 11A-B: ae); opening of duct very small, in median region of the ventral surface of the oral tube, just posterior to the mouth (Fig. 11B: ad). **Valve of Leiblein** with about half size of odontophore, inner organization similar to that of *Zemira*, with narrow folds of the oblique furrow disappearing gradually at anterior and posterior ends (Figs. 11A-B, 12B: vl). **Middle esophagus**, narrow, roughly equal in length to the anterior esophagus, walls thin, inner surface smooth (Figs. 11A-B: em). **Gland of Leiblein** brown, long, triangular, anterior region wide, narrowing gradually towards posterior, posterior tip narrow and rounded; anterior aorta crossing through this gland between middle and anterior thirds (Figs. 10C, 11A: gl). The portion of the duct of the Gland of Leiblein that is free from the gland is relatively long (about half the length of the middle esophagus) (Figs. 11A, 12C: ld); inner surface with a longitudinal, white gland in its dorsal side, and a smooth, thin region on the ventral side; lacking transverse septa within (Fig. 12C). **Posterior esophagus** narrow, about three times as long as anterior esophagus, wall thin, inner surface smooth or with narrow longitudinal folds, close to each other (Figs. 11A: ep; 12D-E: es). **Stomach** trapezoidal, weakly dorso-ventrally flattened, occupies about half of visceral whorl volume, is situated about 1/4 whorl posterior to kidney (Figs. 12D-E); esophagus joins the stomach at left-anterior end, the intestinal joins the stomach to the right of the esophagus, and is slightly wider. Duct to digestive gland single, located a short distance posterior to esophageal insertion and intestinal origin; duct with very wide and flat base, with branches running from opposite sides after short distance. Gastric walls thick muscular. Gastric inner surface with transversal, low, broad, somewhat irregular folds (Fig. 12E). **Intestine** almost straight, weakly sigmoid, running anteriorly (Figs. 10D, 12D-E); inner surface full of low, narrow, closely spaced longitudinal folds; A larger pair of adjacent folds run along the left side of the stomach, gradually disappearing into rectum. Intestine passes initially through digestive gland, then through the ventral flap of the kidney lobe. Rectum and anus as described above (pallial organs).

Genital system. Male (Figs. 10A-B, 13A-B). Testis as described above (visceral mass). Seminal vesicle very large, occupying the columellar surface of almost the entire last whorl of the visceral mass, forming a relatively narrow, extremely convoluted tube (Fig. 10A: sv). Seminal vesicle abruptly terminates near the pallial cavity, giving rise to a very narrow vas deferens that crosses the afferent renal vessel dorsally, and becomes exposed in the pallial cavity, lying along the posterior and right pallial cavity edges, gradually becoming thicker (Fig. 10A). No prostate gland differentiable. Vas deferens descends to pallial floor at mid length of the pallial cavity. The portion of the vas deferens lying on pallial floor is open (furrow); with tall, thick edges (Fig. 10B), becoming convoluted near the base of the penis. Penis of about 1/4 of pallial cavity volume (Fig. 10B); twisted inwards in basal region, middle region slightly broader, constricting gradually up to narrow, rounded tip. Penis duct

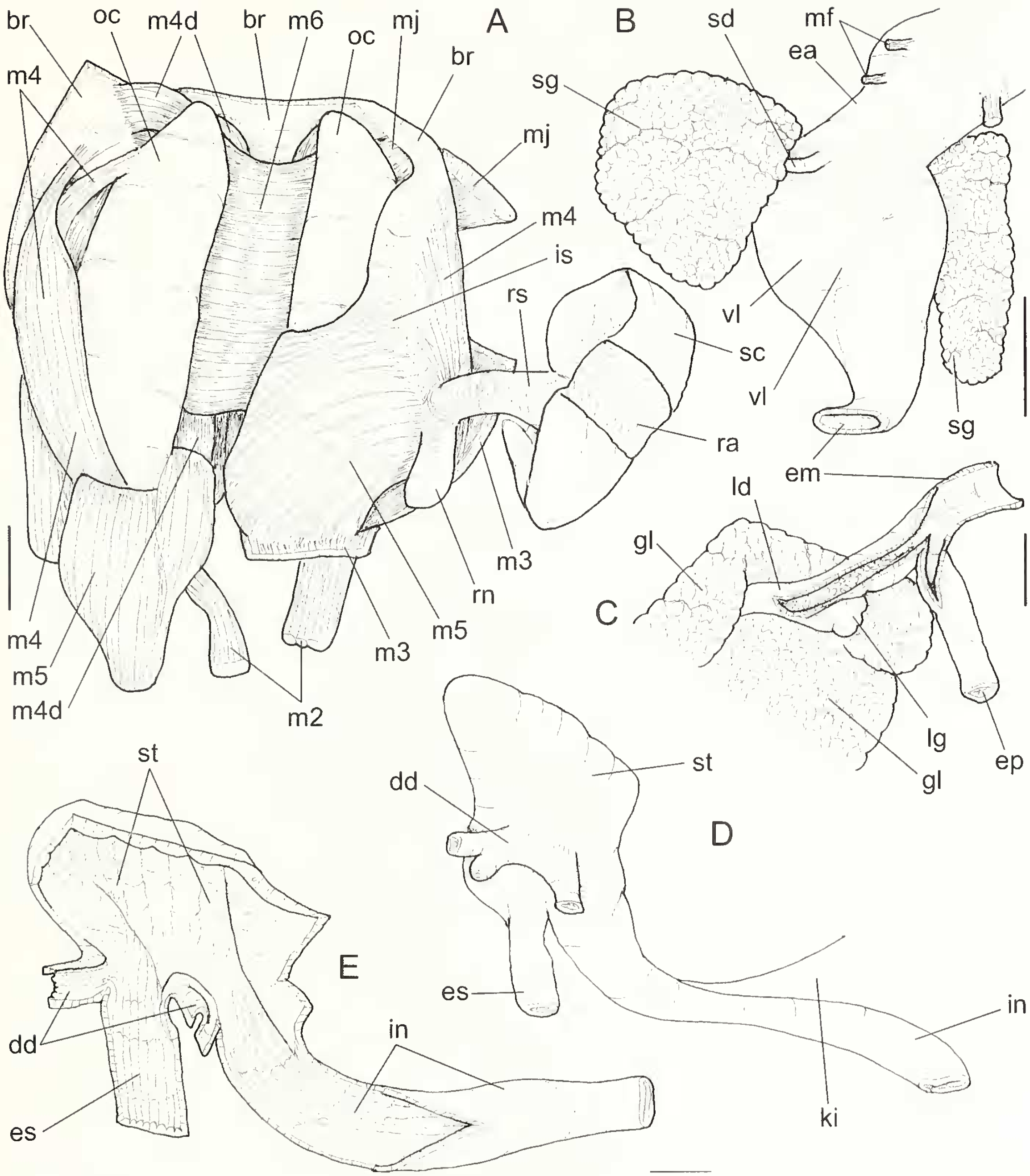

Figure 12. *Fulmentum ancilla* anatomy. A, odontophore, dorsal view, most of the superficial membrane and muscles removed, radular sac deflected to right, both cartilages (oc) deflected from each other, left m5 turned downwards. B, region of the valve of Leiblein (vl), ventral view. C, region of duct of the gland of Leiblein (ld), ventral view, most tubes opened longitudinally. D, midgut as *in situ*, ventral view, position of kidney indicated. E, same, most tubes opened longitudinally to expose inner surface. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

open (a furrow), lying on inner penis edge, relatively deep, runs up to penis tip (Fig. 13A). Terminal papilla in penis tip, about 1/6 of penis length, located inside a chamber formed by terminal portion of penis (Fig. 13B).

Female (Figs. 13C-D). Visceral structures similar to those of males. Visceral oviduct very narrow, running along the middle of the columellar surface of the visceral mass. Visceral oviduct inserting in left side of pallial oviduct, an-

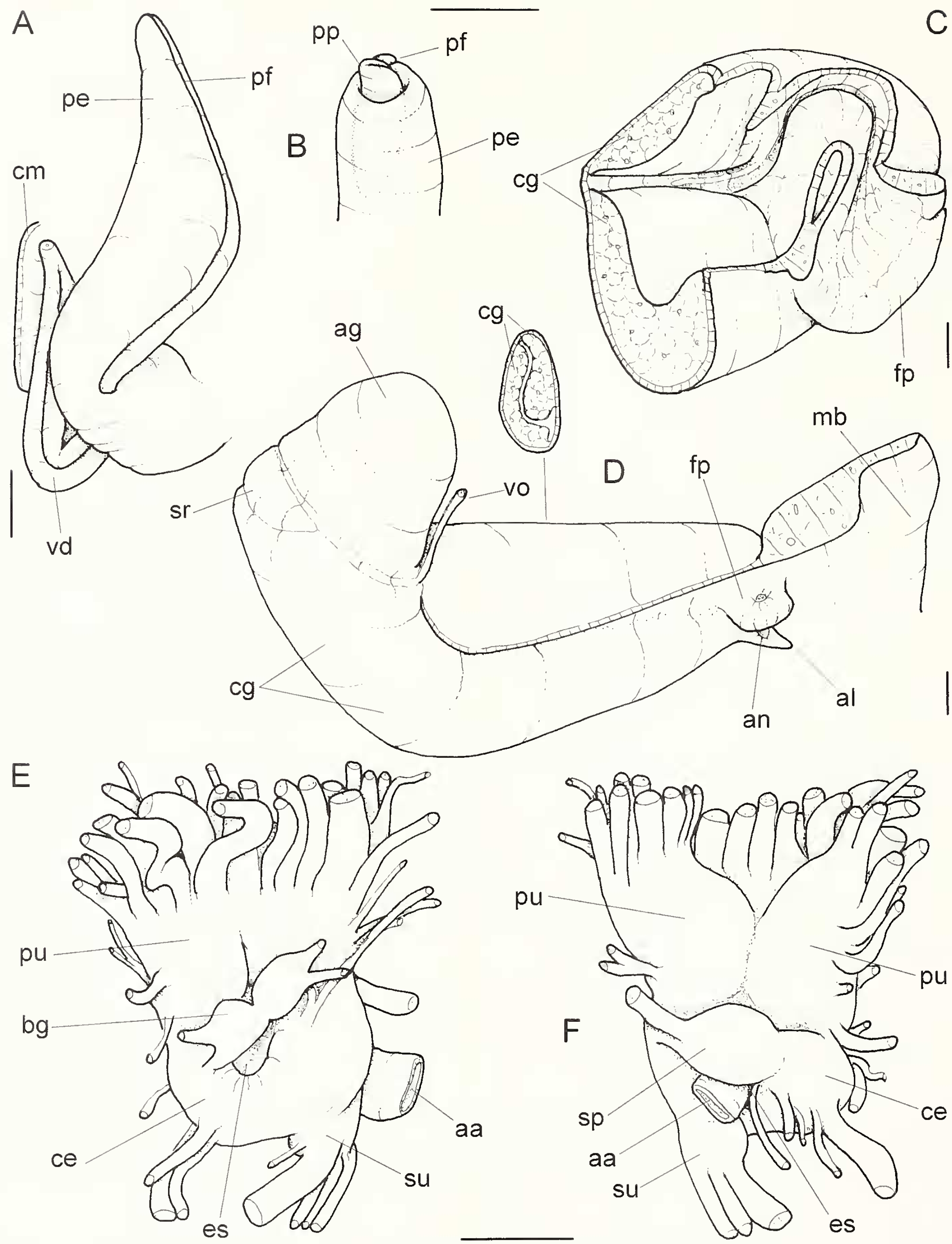

Figure 13. *Fulmentum ancilla* anatomy. A, penis and adjacent region of its base, dorsal view. B, detail of penis tip, showing, partially by transparency, terminal papilla. C, pallial oviduct, ventral view, detail of its terminal region mostly opened longitudinally, walls reflected. D, entire pallial oviduct, ventral view as *in situ*, some adjacent structures also shown, a transverse section at indicated level also shown. E, central nervous system, ventral view, esophageal passage indicated (es). F, same, dorsal view. Scale bars A, D = 2 mm; others = 1 mm. Abbreviations listed in section with figure captions.

terior to albumen gland, opening to vaginal duct. Albumen gland whitish, about ¼ length of pallial oviduct, forming a blind-sac with thick walls and flat lumen that is continuous with the lumen of the capsule gland. Seminal receptacle triangular, located between albumen and capsule glands, close to right-dorsal side, no apparent duct, opening directly to vaginal duct between both glands. Capsule gland beige, inner lumen broad and flat (as wide as gland). Vaginal duct lying all along capsule gland left edge, separated from it by a low fold of dorsal lamina of capsule gland. Capsule gland laminae terminating close to genital pore, without forming a vestibule. Female pore protruded, rounded, located to right of anus. Female pore walls thick muscular, inner lumen flat, curved from left to right, then to left again, expanding gradually, leading to pore (Fig. 13C). Female pore edges thick, preceded by longitudinal, broad folds. No cement gland in sole of foot.

Central nervous system (Figs. 13E-F). Located at base of proboscis, a short distance ventral to the rhynchostome. Very concentrated, practically no individual ganglia distinguishable. Cerebro-pleural ganglia widely connected to each other along median line. Both also widely connected to pedal ganglia, no connective distinguishable. Pedal ganglia of about the same size as the cerebro-pleural ganglia. Commissure between both pedal ganglia relatively narrow and very short (both pedal ganglia maintained in contact). Pair of buccal ganglia small, close to each other, located obliquely (left ganglion slightly more anterior) in dorsal region of cerebro-pleural ganglia; connective with cerebral ganglia narrow and short, left connective a little longer and joining another secondary nerve, running anteriorly. Supra- and subesophageal ganglia about half the size of the main ganglia, located near and ventral to right cerebral ganglion; subesophageal ganglion connected to cerebral ganglion by a narrow and short connective; supra-esophageal ganglion connected to subesophageal ganglion by a broad and very short connective, and also to left cerebral ganglion by a narrow and short connective.

Measurements of shells (in mm). NMSA E5279: 64.5 by 35.0.

Distribution. South Africa.

Habitat. Rocks and coarse sand, from 32 to 81 m depth.

Material examined. SOUTH AFRICA. **Western Cape**; 93 km SE of Mossel Bay, 68.4 m depth, NMSA E2770, 1♀ (no shell) (Exch. C. Marais col., 24/vi/1988), SW of Mossel Bay, Agulhas Bank, 81 m depth, NMSA E5279, 1♀ (Exch. C. Marais col., xi/1988); Struis Bay, 34°47.2'S 20°08.6'E, 32 m depth, NMSA S3578, 1♂ (no shell) (dredged Sardinopsis, 08/vi/1991).

Discussion. *Fulmentum ancilla* has been mostly referred in the genus *Pseudoliva* or *Sylvanocochlis* Melvill, 1903, for which it is type species. Recognition of *Fulmentum* is based on the arguments of Vermeij (1998: 60), who considered both genera (*Sylvanocochlis* and *Fulmentum*) as synonyms. Kantor's (1991) anatomical description was used as the ground plan for the anatomical study of this species. Results of the present study generally agree with Kantor's data; the few different points include the presence of transversal distinct folds in the hypobranchial gland found in his specimens (his fig. 12D), but lacking in those examined here.

Genus *Melapium* Adams and Adams, 1853
(Type species *Pyrula lineata*, by subsequent designation of Cossmann, 1901)

Melapium lineatum (Lamarck, 1822)
(Figs. 9F-K, 4E-F, 14A-17F)

Melapium lineatum: Liltved 1985: 9; Kantor 1991: 39-41 (figs. 1A-B, 2B, 17, 18); Hayes 1994: 77-78; Vermeij 1998: 75.

Description

Shell (Figs. 9F-K). Of medium size (about 30 mm), rounded; wider than long. Walls thick. Color cream, with narrow axial bands, dark beige, with irregularly intercalated longer and shorter bands, mainly concentrated in a band along the middle of the body whorl; canal white, with purple pigmentation within the anterior edge. Protoconch flat, dome-shaped, of 1½ whorls; transition to teleoconch indistinct (Figs. 9G-J). Spire flat, low, weakly elevated, with about 3 whorls. Suture relatively deep. Body whorl very large, surrounding almost completely the penultimate whorl. Surface glossy, lacking sculpture except for weakly visible growth lines. Anterior region with carina surrounding left edge of canal, projected forwards. Aperture rounded (Fig. 9F), located close to suture, peristome white, gradually becoming orange in interior regions. Outer lip simple, semi-circular; edge thick, rounded. Inner lip bearing thick callus, covering roughly half of the ventral surface. Canal short, broad, relatively deep, projected forwards. Young specimens (about 2 whorls) antero-posteriorly longer, outline elliptical (Figs. 9I-J); outer surface opaque, sculptured by a net of thin and very narrow reticulation of spiral and axial lines (Fig. 9I).

Head-foot (Figs. 9K, 14A-B, 14 D, 15B). Head weakly protruded, socket-like; basal region of head as short flap. Tentacles located in both ends of this flap; each tentacle long and narrow, with a broader region just above base; tip pointed. Color mostly beige-cream, with bluish band flanked by a narrow bands of red and yellow surround the dorsal surface of foot at its margins (Fig. 9K); tentacles with pale base and orange middle and distal regions. Eyes located on both ends of head-flap, below the base of each tentacle (Figs. 14A, 14D). Rhynchostome in the form of a transversal slit is located between the tentacles (Fig. 14D). Foot very wide and broad; thick in center, gradually becoming thinner toward the periphery, uniformly in all directions. Furrow of

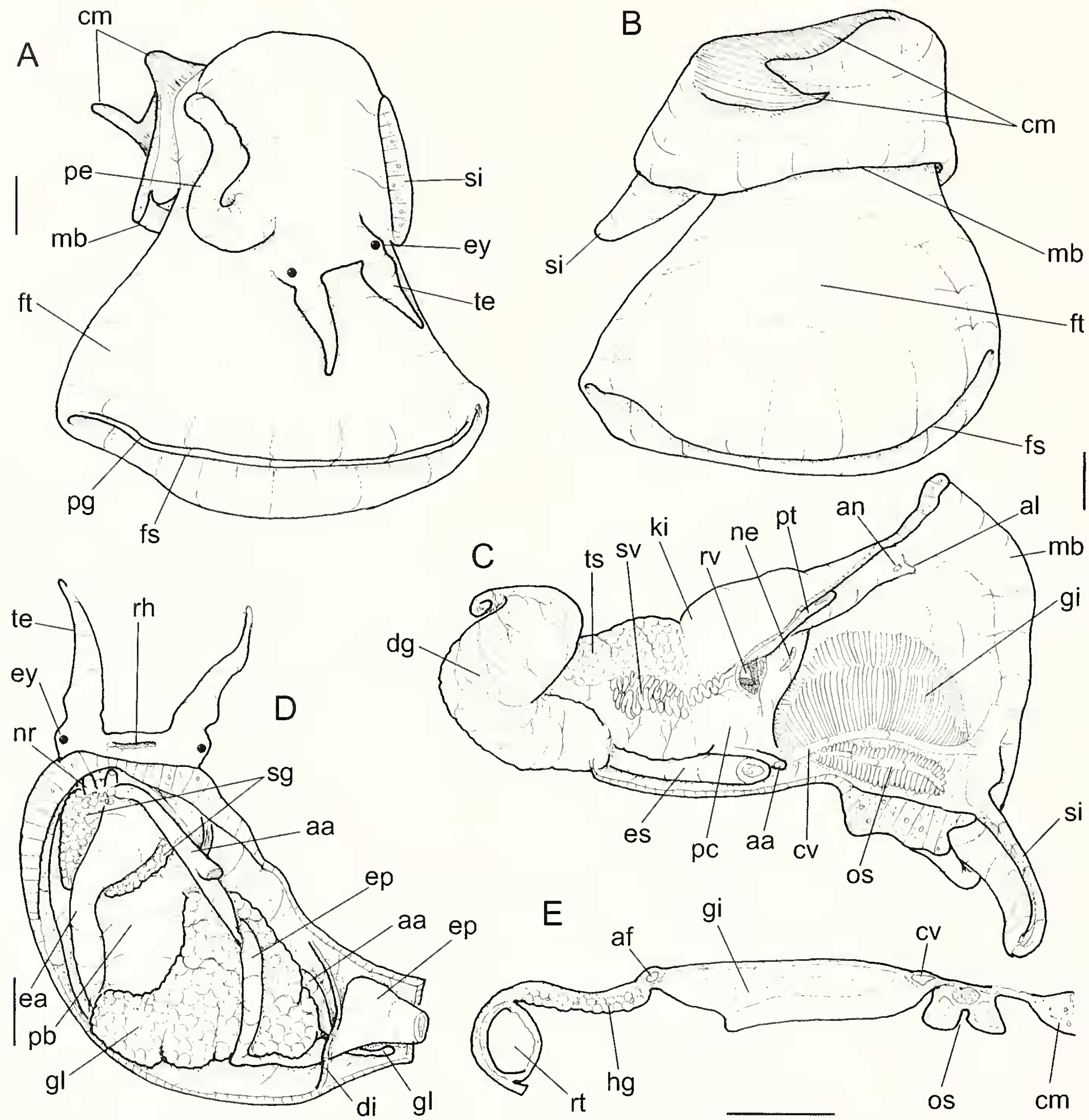

Figure 14. *Melapium lineatum* anatomy. A, head-foot, male, frontal view. B, same, posterior view. C, pallial cavity and visceral mass, male, ventral-inner view. D, head and haemocoel, ventral view, foot and columellar muscle removed. E, Transverse section through pallial cavity roof, at mid-length of the osphradium. Scale bars = 2 mm. Abbreviations listed in section with figure captions.

pedal glands very thin, restricted to anterior half of foot edge (Fig. 14A: pg). Columellar muscle of about 1/3 whorl, having broad main flap in middle and right regions; secondary flap taller and longer, at its left end, projected deeper, weakly coiled (Fig. 12A: cm). Male penis relatively small, originating far removed posteriorly from right tentacle (described below). Haemocoel oval, broad, weakly curved to left (Fig. 14D).

Operculum. Absent.

Mantle organs (Figs. 14C, 14E). Mantle border simple, wide, thick, unpigmented. Pallial cavity broad and short (just over ½ whorl). Siphon long (equal in length to pallial cavity) and slender; edges simple; inner surface with low transversal folds. Siphon base with pair of reinforcements extending as low folds beyond siphon base, parallel to mantle border, longer on right, about 1/3 of mantle border length, gradually diminishing. Osphradium slightly longer than ½ pallial cavity length and about 1/5 of its width; anterior end rounded, posterior end pointed. Osphradium filaments tall, symmetrical, mostly free from attachment to mantle roof (connected mainly to osphradial ganglion), forming a longitudinal concavity along this ganglion. Each filament extends ventrally about twice the diameter of the osphradium ganglion, its edge reinforced by a rod that is weaker along inner regions closer to the ganglion. Gill elliptical and broad, slightly shorter than pallial cavity and about half as wide, slightly curved to left. Anterior and posterior ends broadly pointed, anterior end slightly forward of osphradium margin, and separated from it by a low, broad fold of the siphonal base. Posterior end of gill extends beyond posterior end of osphradium, reaching the pericardium. Gill filaments triangular, relatively low, apex at or slightly to the right of center, rounded; rod broad, lying along left edge, extending slightly beyond the membranous portion of the filament. Ctenidial vein and afferent gill vessel narrow (afferent slightly narrower), running along respective gill edges. Hypobranchial gland moderately thick, cream colored, covering most of the area between the gill and rectum (~1/3 of pallial roof), becoming narrow in the region anterior to the anus, surrounding right edge of gill. Rectum relatively broad, running along the right edge of the pallial cavity for about 2/3 of its length. Anus detached, located between middle and anterior thirds of pallial cavity; with small papilla along its left edge. Genital ducts lying between rectum and pallial floor, described below.

Visceral mass (Fig. 14C). Of about 2½ whorls, rapidly enlarging and almost involute. Right portion of visceral structures encroaching into the right posterior portion of the pallial cavity. Kidney triangular, spanning ~½ whorl along its right border, partially located inside the middle and right portion of the posterior pallial cavity. Pericardium located slightly to the left of the middle of the posterior portion of the pallial cavity. Stomach located about 1/3 whorl posterior to kidney, occupying about half of adjacent visceral whorl volume. Digestive gland orange, extending from apex to kidney, surrounding middle digestive tubes. Gonad within right and columellar surfaces of visceral mass, of the same color as the digestive gland all along its length. Ovary surrounded entirely by digestive gland, becoming internal to it.

Circulatory and excretory systems (Figs. 14C, 15A). Heart volume about 1/3 kidney volume; characters similar to those described for *Zemira*, auricle small, entirely attached along antero-dorsal region of pericardium; ventricle very large, intensely muscular. Anterior aorta 5-6 times thicker than posterior aorta. About half of the kidney encroaches into the pallial cavity roof. Nephridial gland relatively thick (thicker anteriorly), covering entire middle and dorsal region of reno-pericardial membrane. Renal lobe similar to *Zemira*, but with more developed transverse, irregular folds; ventral and dorsal flaps of renal lobe with tall folds intercalating with each other successively along their right region. Rectum passes through ventral flap of renal lobe. Dorsal flap of renal lobe hard and yellowish; ventral flap whitish and softer. Renal efferent vessel very large (almost as large as anterior aorta); running from posterior end of haemocoel, penetrating intro renal chamber with left side broadly attached to middle region of pericardium, before giving rise to multiple branches that become progressively smaller and insert between renal lobe folds. Nephropore a transversal slit, with muscular edges, located in middle of reno-pallial membrane; internally free from folds or vessels inserting close to it.

Digestive system (Figs. 15B-16E). **Proboscis** relatively short (about 1/3 of haemocoel length) and narrow (about half of its width) (Figs. 14D, 15B). Several narrow proboscis retractor muscles surround it almost completely, but more concentrated in dorsal-right region, originating in anterior and middle surfaces of haemocoel (Fig. 15B). Proboscis wall very thick in rhynchodeal region, relatively thin in buccal mass region (Fig. 15D). **Mouth** transverse in proboscis tip. **Oral tube** relatively long (about same length as odontophore) and narrow; inner surface with a broad pair of dorsolateral folds, each fold with about 1/3 of oral tube surface, anterior end of each fold rounded, narrowing gradually posteriorly. A shallow area between both folds is equivalent to that of each fold in width (Figs. 15D-E). A longitudinal platform runs along the ventral surface medially, flat, thick, with weakly elevated lateral edges; remaining surface of oral tube smooth (Fig. 15E: ol). Odontophore tube forms extension of the oral tube (Fig. 15E: oo), ventral platform runs along it up to odontophore; walls thin muscular; length equivalent to that of odontophore.

Odontophore oval, about 1/3 of proboscis length. Odontophore organization and muscles somewhat similar to those described for *Zemira*, distinctions are as follows: Odontophore muscles (Figs. 15E-16D): **m2** pair narrow and thin, also inserting in m4 posterior region; **m2a** absent; **mc** pair very wide, inserting in ventral surface of cartilages surrounding at some distance the m6 insertion (Figs. 16A-C); **m3l**, a thin layer of longitudinal muscles covering the dorsal surface of the odontophore tube from the antero-dorsal edge of the odontophore to the intersection between the odontophore tube and esophagus; **m3t**, a thin layer of transverse muscle fibers covering posterior and ventral surfaces of odontophore (Fig. 16B), posterior to m3a; **m4** pair thinner, originated from posterior edge of cartilages, with fibers splayed to form fan, surrounding cartilages inner surface; **m5**, weakly differentiable from m4, appearing as median continuation of m4; **m6**, thin and relatively narrow, anterior region at level of anterior end of cartilages, posterior end about at middle level of cartilages, inserting into ventro-medial edge of cartilages, except in posterior region where they become gradually wider, inserting in outer cartilages

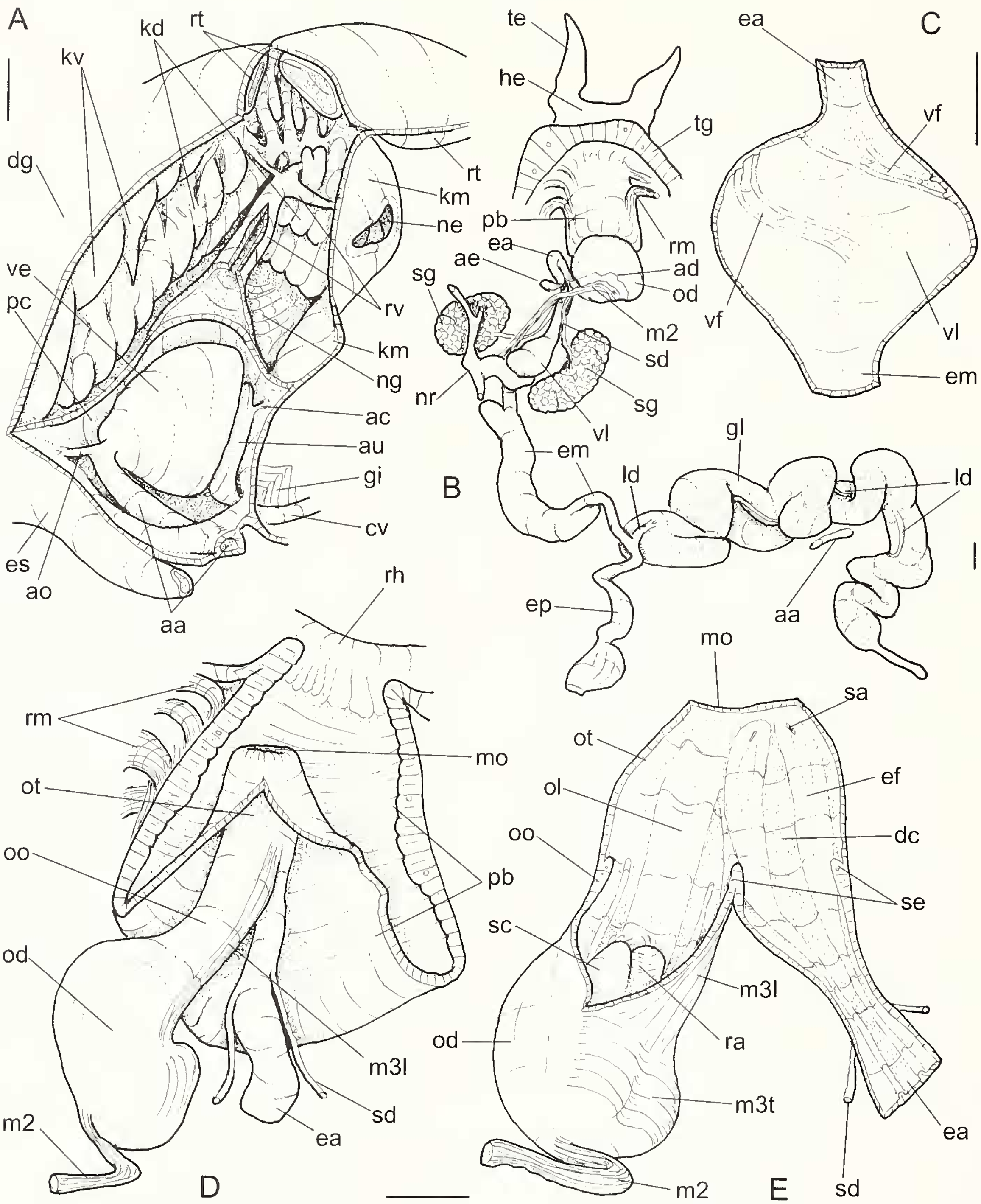

Figure 15. *Melapium lineatum* anatomy. A, anterior region of visceral mass, ventral view, pericardial and renal ventral wall removed, efferent renal vessel (rv) opened longitudinally, rectum (rt) sectioned transversally. B, head and foregut, ventral view, most structures partially uncoiled. C, valve of Leiblein opened longitudinally, its inner structures (gland and valve) removed, only its oblique furrow (vf) remaining. D, proboscis and buccal mass, left view, proboscis opened longitudinally. E, buccal mass, left view, esophagus and odontophore tube (oo) sectioned longitudinally. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

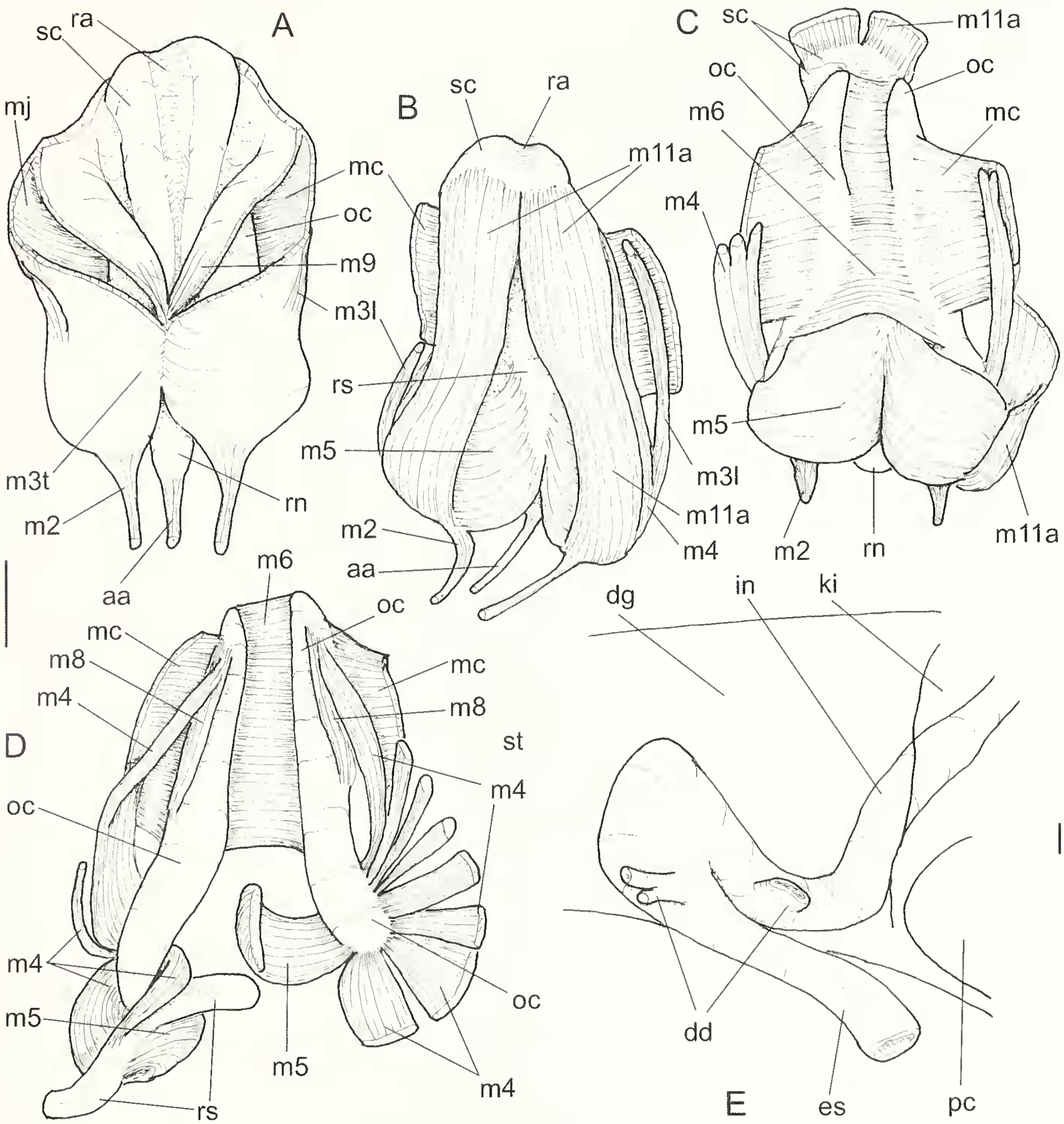

Figure 16. *Melapium lineatum* anatomy. A, odontophore, dorsal view, odontophore tube connecting it to the oral tube opened longitudinally. B, same, ventral view, superficial layer of membrane and muscles removed, circular muscle (mc) sectioned and reflected. C, same, ventral tensor muscle (m11a) sectioned and reflected. D, same, ventral view, radular sac totally removed and reflected downward and to the left, both cartilages and most muscles reflected. E, midgut as *in situ*, ventral view, topology of adjacent structures also shown. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

surface (Figs. 16C-D); **m8**, pair of short muscles on dorsal edge of cartilages (mostly probably part of m4), running attached to dorsal-anterior edge of cartilages, from their anterior region to their middle level (Fig. 16D); **m11a** pair very wide and thin, originating on m4-m5 posterior region (Fig. 16B). Odontophore cartilages (oc) thin and antero-posteriorly long; anterior end broadly pointed; posterior end rounded, uniform in width along their length (Figs. 16C-D). Subradular cartilage (Fig. 16A: sc) relatively narrow, covering only part of odontophore portion exposed in buccal cavity. Radular sac relatively short, slightly longer than odontophore. **Radula** teeth (Figs. 4E-F): **rachidian** tooth wide, spanning 70% of radular width, base wide, boomerang-shaped, with lateral ends rounded, broader than central area, somewhat arched, with 3 pointed, closely spaced, triangular cusps equal in size located in central area, with length equivalent to transverse width of base. Cusps aligned and joined in a single, projected, flat base. Space between rachidian and lateral tooth narrow. **Lateral** tooth hook-like, base about ¼ of rachidian width, gradually narrowing and curving inwards distally, base disposed somewhat obliquely, tip sharply pointed. **Anterior esophagus** originating anterior to odontophore tube, separated from it by a tall septum; inner surface with pair of lateral folds (continuation from folds of oral tube), smooth (Figs. 15B, 15E: ea); three times the length of the odontophore. **Salivary glands** relatively large, as two separated masses, clustered around valve of Leiblein and nerve ring (Figs. 14D, 15B). Salivary ducts very narrow, originating in middle of each gland's median surface, running anteriorly close to anterior esophagus, penetrating the anterior esophageal walls at some distance from oral tube, at the level of the odontophore; then both ducts run within the esophageal walls and inside the dorsal folds of the oral tube; salivary aperture small, in middle region of dorsal folds anterior end (Fig. 15E: sa). **Valve of Leiblein** with about 1/4 of odontophore volume, inner organization similar to that of *Zemira*, but differs in the oblique furrow being wider and shorter, undergoing the entire torsional rotation within the valve walls, ending just beyond the middle portion of the valve and at the same level as it started in region preceding valve (Figs. 15B-C). **Middle esophagus** (Fig. 15B: em) broad, about twice the length of the anterior esophagus, internally 3/4 filled by a whitish gland that lacks an inner septum. This gland lies along a region of esophagus, its anterior and posterior ends forming short blind-sacs that are located at some distance from the anterior and posterior ends of the middle esophagus.

Beyond this gland is a hollow furrow that is separated from the glandular region by a pair of tall and narrow folds. These folds connect with the bases of the blind sacs at both ends of the gland. The remaining middle esophagus (anterior and posterior to gland) a simple tube with thin walls [Kantor (1991: 39) referred to this gland as accessory gland]. **Gland of Leiblein** long and irregularly coiled, somewhat flat (Fig. 15B: gl); width roughly uniform along its length, except for a broader anterior region close to its juncture with the esophagus and very slender, hollow, distal region, with a small, rounded tip. Duct of the gland of Leiblein runs all along its inner surface (Fig. 15B: ld), with a short proximal portion of the duct free of the gland, its inner surface simple, with 7-8 narrow, longitudinal folds. **Posterior esophagus** as long as middle esophagus, anterior half narrow, inner surface smooth, expands abruptly after passing through the diaphragm dividing the haemocoel from the visceral cavity (Fig. 15B: ep), developing 10-12 tall, glandular longitudinal folds, somewhat separated from each other. **Stomach** occupies about half of the whorl volume, forming inflated curve (Fig. 16E); two ducts to lead to the digestive gland, the duct closer to the esophageal insertion is narrow, bifurcating at a short distance from its origin, turned postero-ventrally; the other duct is closer to the intestine, broad, longer anteroposteriorly, turned antero-ventrally. The inner gastric surface is mostly smooth, except some low folds continuing from the posterior esophagus that gradually diminish posterior to esophageal duct to digestive gland. Intestine (Fig. 16E: in) slightly broader than the esophagus, initially running parallel to it. There is no clear demarcation between the intestine and the stomach. In a short distance, the intestine broadens to become as wide as the stomach and curves abruptly toward the right, lying on the posterior renal wall (Fig. 16E). Rectum and anus as described above (pallial organs).

Genital system. Development (Figs. 9F, 9H, 17C). There is evidence to suggest direct development, as most specimens, including males, carry a pair of large egg capsules attached to the anterior region of inner lip (Fig. 9F). Both capsules are equivalent in size and each contains a single specimen with 3 or more whorls (Fig. 9H). Each capsule is long, somewhat cylindrical, with both ends rounded. The capsule wall is flexible, heavy, thin but strong, pale beige in color, and opaque, not transparent. Capsules are attached by a short and wide peduncle, located longitudinally along the side (Fig. 17C). Both capsules remain side by side, situated transversally across the anterior half of the shell's inner lip.

Young specimens removed from capsules show complete development, no operculum and appear to have the capacity for crawling (Figs. 9H-J). Nothing but viscous yolk was found inside capsules, except occasionally a granulose soft tissue surrounding young specimens in early development (Fig. 17C).

Male (Figs. 14A, 17B). Testes located along the columellar surface of the visceral whorls. Seminal vesicle situated ~½ whorl posterior to pallial cavity, consists of a highly convoluted narrow tube that is ⅓ the width of the visceral mass width and runs along the middle, columellar region (Fig. 14C: sv). A narrower region of the seminal vesicle adjacent to the pericardium and afferent renal vessel opens into the middle region of the posterior-ventral end of pallial cavity. Pallial vas deferens gradually becomes open and glandular forming the prostate gland. Prostate gland narrow, opened as a thick walled furrow, running along ventral surface of rectum for about ½ pallial cavity length (Fig. 14C: pt). Pallial vas deferens gradually becoming narrow, crosses to right corner of the pallial floor, as superficial, relatively narrow, protruded furrow, surrounding columellar muscle by a distance equivalent to 1/4 of pallial cavity length; abruptly turning left on pallial floor and entering the base of the penis. Penis long, somewhat flattened; proximal half of

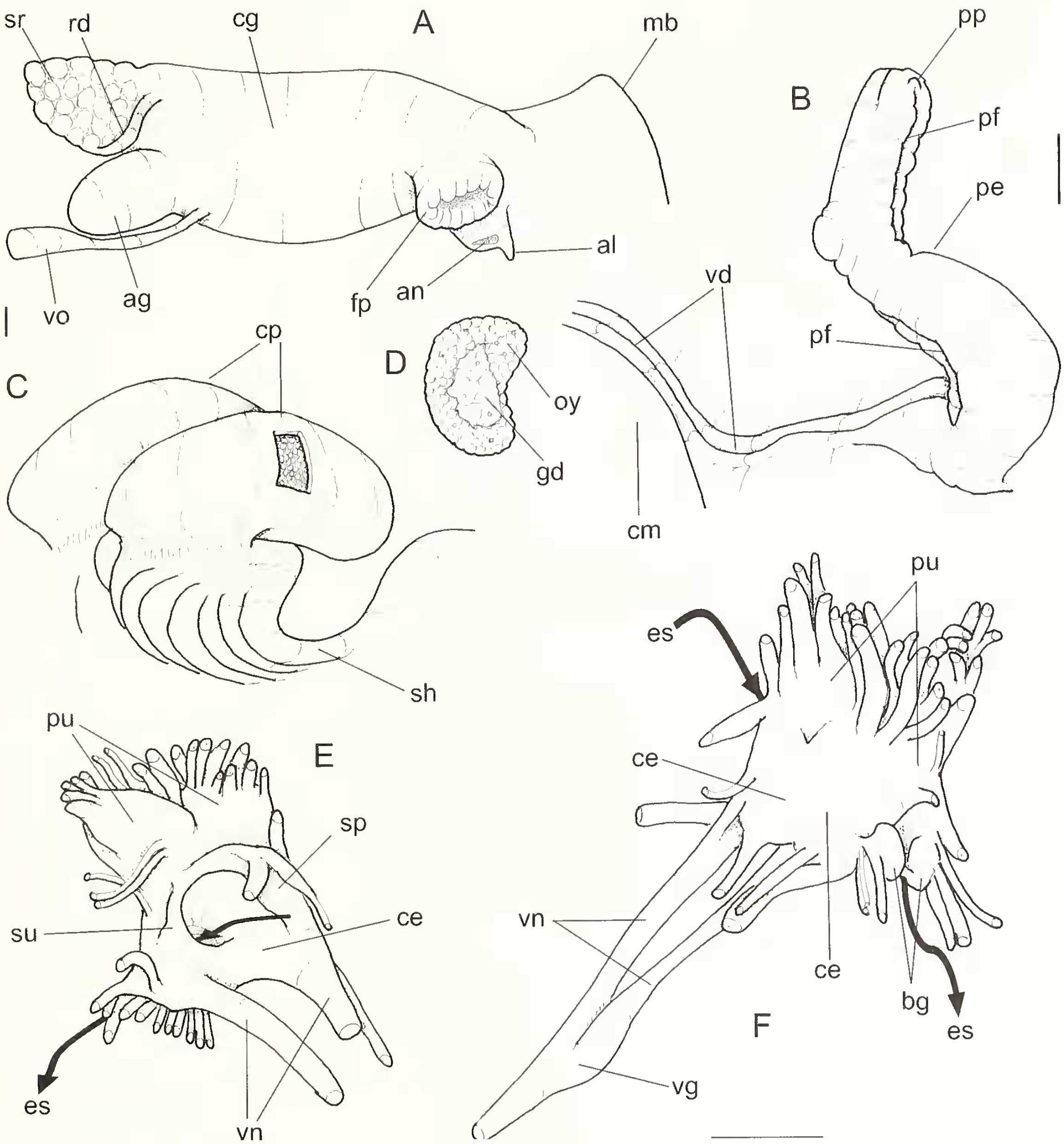

Figure 17. *Melapium lineatum* anatomy. A, pallial oviduct and some adjacent structures, ventral view. B, penis and adjacent region of its base, dorsal view, penis reflected upward. C, anterior region of shell, anterior view, partially showing the siphonal canal and a pair of egg capsules, with rectangular hole cut. D, visceral mass, female, transverse section through middle region of the penultimate whorl. E, central nervous system, ventral, right oblique view. F, same, dorsal, left oblique view, visceral ganglion (vg) included. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

uniform width, with furrow running along its posterior edge; middle region with an irregular surface, furrow crossing to opposite penis edge; distal half about ⅔ as wide as proximal half, with furrow along its anterior edge; penis tip blunt, rounded, furrow leading to a small sub-terminal papilla (Fig. 17B).

Female (Fig. 17A). Ovary occupies entire surface of visceral whorls, covering entirely digestive gland, is thinner along the columellar surface (Fig. 17D). Visceral oviduct very narrow, running along middle ventral surface of visceral mass, running along the left edge of the kidney before entering the left edge of the pallial oviduct, between its posterior and middle thirds. Pallial oviduct with about same length of pallial cavity, protruding into the anterior region of the kidney and separated from mantle border by a distance equivalent to ¼ of pallial cavity length. The albumen gland, a small whitish appendix, comprises about 1/6 the size of the pallial oviduct and is located in the left half of the posterior pallial oviduct, ventral to the kidney, joining the capsule gland through a wide anterior opening. The seminal receptacle is equal in size to the albumen gland, and located alongside it, consisting of small, rounded lobes, several very narrow, iridescent ducts that run from posterior to anterior along left its edge and connect to the posterior end of the capsule gland. The capsule gland occupies most of the pallial oviduct, is yellowish and somewhat flattened dorso-ventrally, consisting of a pair of thick glandular lamellae. The female pore is sub-terminal, situated to the left of the anterior-most portion of the capsule gland at the end of a tall, wide, terminal papilla. Terminal papilla is situated slightly posterior and to the right of the anus, and is preceded by a small, hollow, thick-walled chamber continuous with the capsule gland lumen. There are no signs of a cement gland in sole of the foot.

Central nervous system (Figs. 17E-F). The nerve ring is highly concentrated, and it is difficult to distinguish the ganglia and connectives. Its total volume occupies roughly 1/10 of the haemocoel. The pedal ganglia are equivalent in size to the cerebral-pleural ganglia. The passage of the esophagus is narrow. A pair of buccal ganglia are located close to the cerebral ganglia. Supra and sub-esophageal ganglia are also located close to the nerve ring. The visceral ganglion is located posteriorly at a distance equivalent to the nerve ring length.

Measurements (in mm). NMNH S6362: 24.7 by 22.7; NMNH 59733: 26.5 by 23.6; NMNH V1899: 20.9 by 22.3; NMNH V9979: 26.2 by 24.0.

Distribution. South Africa.

Habitat. Fine sand.

Material examined. SOUTH AFRICA. **Eastern Cape** (dredged R.V. Meiring Naudé); Transkei, off Mbotyi, 31°29′02″S 29°45′04″E, 48-50 m depth 3♀, NMNH V9978, (sta. F5, viii/1981); off East London, 33°06.2′S 27°52.4′E, 70 m depth, 1♂, NMNH V9979 (sta. XX34, 16/vii/1984). **Western Cape**; Agulhas Bank, E of Martha Point, 34°29.5′S 20°33.3′E, 28 m depth, 1♂, NMNH S6362 (NMDP CC13, 7/iv/1991), 34°29.5′S 20°32.9′E, 24-28 m depth, 1♂, NMNH 59733 (MMDP CC14, 7/iv/1991); South Cape, south of Cape Infanta, 35°38′S 20°50′E, 90 m depth, 1♂, NMNH V1899 (MMDP sta. A16590D, 30/ix/1994).

Discussion. The genus *Melapium* was removed from Pseudolividae by Kantor (1991) and Vermeij (1998), based on anatomical and conchological peculiarities. One of the more conspicuous differences is the lack of spiral groove at the outer lip and the prominent entrance of the siphonal canal. Kantor (1991) erected a new family, the Melapiidae, to include this genus. Vermeij (1998), on the other hand, argued that *Melapium* can be placed in the Strepturidae. As several authors still include this genus in the Pseudolividae (OBIS 2004), this assignment is tentatively maintained here.

This study was built upon the anatomical description of Kantor (1991), but expanded to include developmental data and the different strategy of carrying the egg capsules.

Family Nassariidae

Genus *Nassodonta* H. Adams, 1867

(Type species *Nassa insignis* H. Adams, 1867, by monotypy)

Nassodonta dorri (Watteblet, 1886)
(Figs. 3G-J, 4G-I, 18A-19D)

Canidia dorri Watteblet, 1886: 56-57 (pl. 4, fig.2).
Nassodonta dorri: Kantor and Kilburn 2001: 99-104 (figs. 1-21).

Description

Shell (Figs. 3G-H). Fusiform, up to 15 mm; color greenish beige, with some sparse, weak, pale brown chevrons on the body whorl. Walls very thick. Protoconch eroded. Spire of about 4 convex whorls; suture deep; last two spire whorls with strong axial nodular threads, gradually disappearing towards body whorl. Body whorl mostly smooth except for growth lines; ventral region with about 5 wide, uniformly spaced, spiral furrows along its anterior half, the inferior furrow widest, encircling the siphonal canal. These furrows continue onto the dorsal surface of body whorl. The posterior furrow is wider, producing a small projection on the outer lip. Aperture elliptical, peristome whitish. Inner lip smooth, thick, lacking callus. Outer lip thick, blunt, with 2 or 3 low teeth along its central area. Canal wide, short, simple. Other details in Kantor and Kilburn (2001: 101).

The following description is based on re-hydrated semi-mummified specimens.

Head-foot (Figs. 18A-B). Head-foot consists of 1½ conical whorls. Head not obvious and inlaid, marked only by presence of tentacles. Tentacles about ½ as long as the foot, the proximal ⅔ clearly broader than distal ⅓. Eyes are well developed, located at outer sides tentacle prior to narrower region. The broad optical nerve is easily seen by transparency, running along the center of each tentacle. Tentacle bases adjacent. Each tentacle located close to each other, running parallel like a socket. Rhynchostome very narrow, located just ventral to region between tentacle bases. Foot wide, ample, simple, occupying about ⅓ of shell volume when retracted. Retraction is umbrella-like, producing a ventral concavity. The anterior furrow of pedal glands is surrounded by thick edges that are restricted to the anterior border of the foot, weakly expanding laterally. Ventral mantle insertion far posterior to pedal edges. Columellar

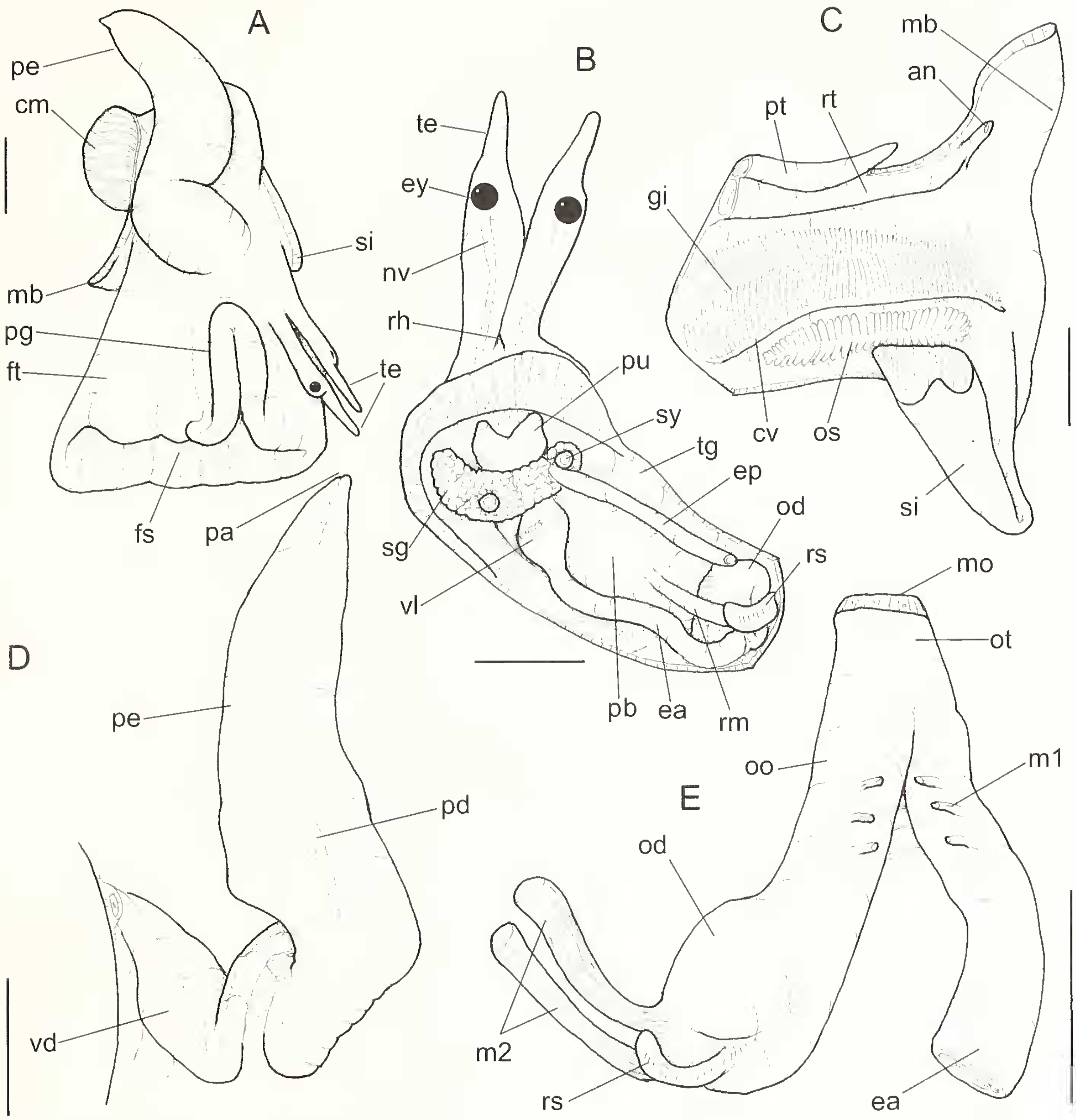

Figure 18. *Nassodonta dorri* anatomy. A, head-foot, male, frontal view. B, head and haemocoel, ventral view, foot and columellar muscle removed. C, pallial cavity, male, ventral-inner view. D, penis and adjacent region of its base, ventral view, penis partially reflected, portions of penis duct (pd) seen by transparency. E, buccal mass, left view. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

muscle simple, of about ¾ whorl. Male with large penis inserted posterior to right tentacle, at short distance from median line. Haemocoel elliptical, relatively wide, oblique.

Operculum (Figs. 3I-J). Corneous, pale brown, elliptical, occupying entire aperture. Nucleus sub-terminal, anterior. Outer sculpture concentric, with weak spiral growth lines. Inner surface glossy; scar elliptical, deep, closer to inner edge, occupying about half of opercular area. Other details in Kantor and Kilburn (2001:101, fig. 14).

Mantle organs (Fig. 18C). Mantle border simple, somewhat thick, whitish. Siphon thick, short, conical, with simple edges, about ½ of pallial cavity length. Pallial cavity spans about 1 whorl. Osphradium long, elliptical, with an area equivalent to ⅓ of gill area, left filaments about half the size of the right filaments; anterior end rounded, located at base of siphon; posterior end pointed. Gill spans about ½ of pallial roof area, adjacent to the osphradium. Its anterior end is pointed, but broadens at first rapidly then gradually until the posterior ⅓ of the pallial cavity then narrowing gradually. Gill filaments are low, triangular, and have a central apex. The roof of the pallial cavity separates the gill from the rectum, which is narrow and runs along the right edge of the pallial cavity. The anus is simple, at the distal end of a short, detached portion of the rectum, at the level of the anterior end of the gill.

Visceral mass. Not seen.

Circulatory and excretory systems. Not seen.

Digestive system (Figs. 18B, 18E-19D). The proboscis is narrow, thin walled, about ¾ of the head-foot length (Fig. 18B: pb) with a thick muscular, sphincter-like base (Fig. 19A). Proboscis and buccal mass relatively short, with about ⅓ remaining in the retracted proboscis. Odontophore about ½ of proboscis length, about ½ protruding beyond the proboscis in retracted position. The oral tube with is about ½ the odontophore length and width, its inner surface smooth and simple. The odontophore and esophagus detach from each other just posterior to oral tube, but are bound to each other by a series of narrow lateral muscles (mt). Odontophore muscles (Figs. 18E-19D): **m1**, small muscles connecting lateral edge of odontophore tube with adjacent region of esophagus; **m2**, strong pair of buccal mass retractor muscles, originating from ventral surface of haemocoel, running anteriorly, mostly attached to ventral surface of the proboscis, inserting into the posterior end of the cartilages; **m2a**, pair of strong accessory buccal mass retractor muscles and accessory dorsal tensors of the radula (Figs. 19C-D), originating in same region as m2, running medially alongside the m2 pair, attached to the ventral surface of the proboscis, becoming broader after penetration into odontophore, inserting along lateral surfaces of radular sac; **m3**, superficial and thin pair of muscles, originating in dorsal region of m2a pair, in a region just anterior to their penetration into the odontophore, running along superficial membrane covering odontophore, splaying along anterior region of this membrane; **m4**, pair of strong dorsal tensor muscles of radula, originating in medial, dorsal, and posterior surfaces of cartilages, running anteriorly, inserting into the radular sac with m2a; **m4d**, narrow pair of accessory dorsal muscles of radula, having same parameters as m4 but running more dorsal, originating more dorsal and anterior to m4 origin, and inserting more medially, covering m4/m2a insertion; **m5**, pair of ventro-medial dorsal tensor muscles of the radula, originating on the outer-ventral surface of the posterior end of the cartilages (opposed to m4 and m4a origins), running anteriorly, covering the ventral surface of m4/m2a, inserting along the radular sac with m4/m2a; **m6**, thin, horizontal muscle, connecting both cartilages along their median-ventral edges, from a region just posterior to cartilages join, spanning roughly half the length of the odontophore, narrow anteriorly, gradually broadening posteriorly. **mj**, a pair of narrow odontophore protractor muscles, originating along the odontophore anterior tube (that connects odontophore to oral tube), gradually becoming thicker posteriorly, inserting in odontophore cartilages along the middle region of their dorsal edge; **mc**, circular muscle opposing m6, inserting along outer-dorsal edge of both cartilages (opposite to m6), surrounding dorsally all inner muscles (except m11a); **m11a**, pair of narrow ventral tensor muscles of the radula, originating on the median-dorsal region of the cartilages, just anterior to m4 origin, running anteriorly, covering mc, inserting into the ventral end of the subradular membrane (Fig. 19C). Subradular cartilage (**sc**) is a convex membrane covering the anterior region of the odontophore, protrudes into the buccal cavity (Fig. 19C). Odontophore cartilages (**oc**) are paired, long, narrow, flat, slightly broader anteriorly (Figs. 19B-C); their posterior ends rounded, narrow; fused along ventral edge along the anterior ¼ of their length. Radula about 1½ times odontophore length. Radular teeth (Figs. 4G-I): **Rachidian** arched, flat, spans ½ of radular ribbon width; with ~10 sharp, pointed cusps along the cutting edge, somewhat similar to each other, slightly shorter towards tooth margins, separated from each other by space equivalent to their size. Secondary, irregularly disposed, small cusps are sometimes present, mainly along the median region; lateral edge straight, ⅓ of rachidian width; posterior edge concave, well separated from neighboring tooth. **Lateral teeth** with a rectangular base about ⅔ as wide as the rachidian tooth, separated from rachidian tooth by a gap about 1/8 of the radular ribbon width. Lateral teeth are situated obliquely as if continuations of the rachidian tooth, each with ~5 broad cusps along its cutting edge. Cusps similar in size except for outermost cusp, which is about 3 times the length and slightly broader than remaining cusps. Outermost cusp curved inward. Innermost cusp with up to five very small secondary cusps along its inner edge. Other details of radula as reported in Kantor and Kilburn (2001: 101-102, figs. 15-20). **Salivary glands** are whitish, amorphous, and restricted to the anterior region of haemocoel, surrounding the proboscis base and nerve ring. Neither their ducts nor the accessory salivary glands were found (Fig. 18B: sg). The anterior esophagus (Fig. 18B: ea) is narrow, originating from the oral tube (ot) after a distance equivalent to half the length of the odontophore. 3-4 pairs of narrow, well-separated slender pairs of jugal muscles connect the lateral surface of anterior esophagus to the lateral surface of odontophore tube (Fig. 18E: m1). Inner surface of anterior esophagus smooth. Anterior esophagus length equivalent to that of the proboscis. Valve of Leiblein about ¼ odontophore volume in size, located just posterior to nerve ring, at the ventral base of the proboscis

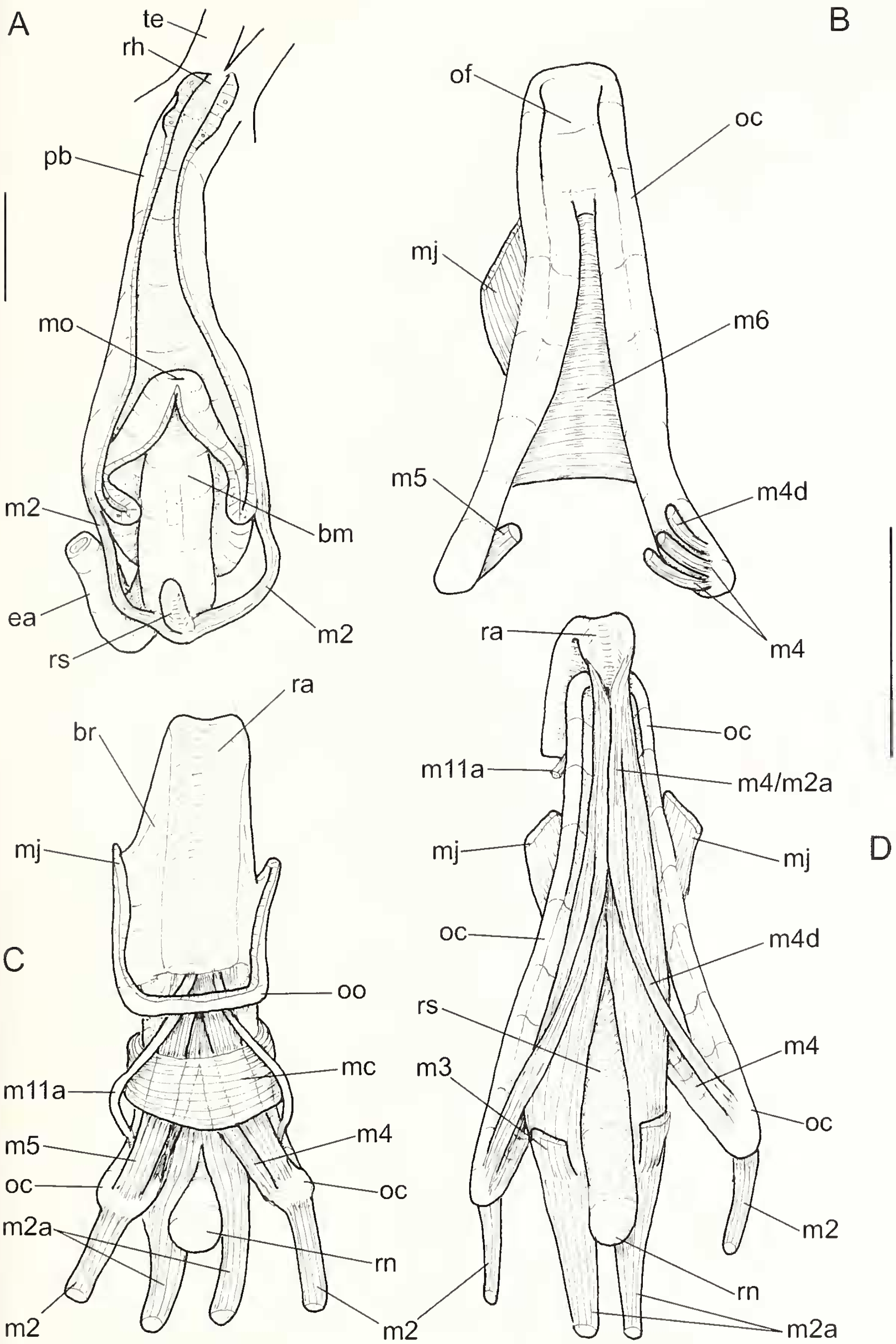

Figure 19. *Nassodonta dorri* anatomy. A, foregut, ventral view, proboscis (pb) opened longitudinally, head region also shown. B, odontophore cartilages, dorsal view, insertion of some muscles also shown. C, odontophore, ventral view, superficial layer of membrane and muscles partially removed, structures of posterior region partially reflected. D, same, dorsal view, superficial layer of membrane and muscles removed, ventral portion of radula partially reflected forwards. Scale bars = 1 mm. Abbreviations listed in section with figure captions.

(Fig. 18B). the gland of Leiblein was not found. The posterior esophagus is narrow, running along the left side of the haemocoel. Midgut not examined. Rectum and anus are described above (pallial cavity).

Genital system. Male (Figs. 18A, 18D). Visceral structures not examined. Prostate gland narrow, closed (tubular), running ventral to and to the right of the rectum for 3/4 of its length (Fig. 18C: pt) before narrowing and abruptly crossing to the pallial floor. The pallial vas deferens is broadest just after descending to the pallial floor, narrows and forms a zigzag on the surface of the pallial floor leading to the penis base (Fig. 18D: vd). The penis is about half as long as the head-foot (Fig. 18A), its base twisted and oval in section. The penis widens somewhat abruptly at mid-length forming a blunt bulge along its right edge. The median and distal thirds of the penis are flat (Fig. 18D), gradually tapering to a pointed tip. The penis is duct narrow, running medially to the penis tip, where it opens.

Female. No well-preserved female examined. Visceral structures not seen. The pallial oviduct is whitish, closed (tubular), about twice the width or the rectum, and apparently lacks an anterior bursa copulatrix. The sole of the foot of females with a thick walled, whitish, glandular cement gland situated medially in the anterior half of the foot, as deep as half the foot width.

Central nervous system. Only pedal ganglia well-preserved, located in ventral region of proboscis base close to each other and to median line (Fig. 18B: pu). Each ganglion occupies a volume about 1/8 of the odotophore. Statocysts with large statolith, each located in the ventral haemocoel surface; partly immersed in the salivary glands and partly in the local pedal musculature.

Measurements of shells (in mm). MZSP 53533: ♂1: 13.6 by 8.6; ♂2: 12.0 by 7.7; ♂3: 12.0 by 8.0; ♀4: 14.2 by 8.3.

Distribution. Vietnam.

Habitat. Brackish, practically freshwater muddy environment.

Material examined. VIETNAM; Kolan, MZSP 53533, 2 shells, 3♂, 2♀ re-hydrated soft parts, Gemert private collection, 3 shells (beach of river).

Discussion. The shell of *Nassodonta* is easily confused with that of pseudolivids, being virtually identical to that of the genus *Macron* H. and A. Adams, 1853. It differs conchologically mainly in having a shorter spire. As discussed by Vermeij (1998: 70-71), *Macron* was referred to the Nassariidae. Based on its anatomy, *Nassodonta* undoubtedly belongs to the Nassariidae–Buccinidae, mainly on the basis of odontophore features.

CHARACTERS

Shell

1. Shell spiral furrow at last whorl: 0 = absent; 1 = present (*Zemira, Fulmentum, Benthobia, Nassodonta*) (CI = 50; RI = 50).

   The spiral furrow dividing the shell body whorl traces the position of the labral tooth on the outer lip, although this tooth is not well-developed in all species. It is normally present as a shallow, oblique furrow between the middle and anterior thirds of the body whorl. This furrow is one of the more conspicuous pseudolivid shell features, and has been called as "pseudolivid groove" (Vermeij 1998).

   However, some taxa considered to be pseudolivids, such as *Melapium*, lack this furrow, while a furrow and labral tooth is present in other genera that unquestionably belong to other families. Some examples include: *Acanthina* Waldheim, 1807 (Muricidae); *Leucozonia* Gray, 1847 (Fasciolariidae); *Ancilla* Lamarck, 1799 (Olividae); and *Bivetiella* Wenz, 1938 (Cancellariidae). These indicate the high degree of convergence in this character.

2. Tooth on outer lip: 0 = absent; 1 = present (*Zemira, Fulmentum*) (CI = 50; RI = 0).

   Although the furrow normally is associated with a tooth at the outer lip, also called labral tooth, this character only refers to a well-developed one, and not to a small projection. Apparently, the tooth at the outer lip is associated with predation on bivalves, serving to separate the valves. In the present study, it is equally parsimonious to consider state 1 as supporting node 4 reverting in node 6 or as a convergence between *Zemira* and *Fulmentum*, the first hypothesis is shown in the Fig. 1.

3. Determinate growth: 0 = present; 1 = practically absent (*Melapium, Fulmentum, Nassodonta, Benthobia*) (CI = 33; RI = 0).

   Determinate growth is the development of a differentiated peristome when the animal becomes mature. This feature is well explored by Vermeij and Signor (1992) and is here applied. As determinate growth is present in most of higher Caenogastropods (Simone 2000), it is considered plesiomorphic for neogastropods, and its absence, *i.e.*, the non-determinate growth is here considered a derived reversal. As some species considered in state 1 have a weak thickness of the outer lip, the word "practically" is introduced.

Head-foot

4. Cephalic tentacles: 0 = separated (*Melapium, Benthobia*); 1 = joined to each other (*Nassodonta, Fulmentum, Zemira, Siratus*) (CI = 50; RI = 66).

   The cephalic tentacles placed together, close to the median line. This kind of modification is different from the normal feature in higher caenogastropods, which possess the state 0.

5. Foot posterior furrow: 0 = absent; 1 = present (*Benthobia*) (CI = 100; RI = 100).

   The conspicuous posterior furrow on the sole of the foot is restrict to the genus *Benthobia* and may be a character of the genus. It is discussed in Simone (2003).

6. Columellar muscle: 0 = simple; 1 = double (with a siphonal branch) (*Siratus, Melapium*) (CI = 100; RI = 100).

The posterior region of the columellar muscle is normally a simple and broad flap. However, in the species listed under state 1, this region is bifid, having a wider left branch and another slender and taller right branch (Figs. 14A-B: cm). This feature has been commonly found in muricids according to my experience, and is related to an anterior furrow internally on each whorl, maintained by the siphonal canal, into which the right branch fits.

7. Operculum nucleus: 0 = terminal (*Fulmentum, Benthobia*); 1 = sub-terminal (*Nassodonta, Zemira*); 2 = almost central (*Siratus*); 3 = absent (*Melapium*) (CI = 75; RI = 0; not additive).

An operculum with a terminal nucleus is a modified condition in gastropods, but among the neogastropods, this is the plesiomorphic condition. The remaining states, including the loss of the operculum, are considered further modifications. While the loss of the operculum is certainly a different phenomenon from the position of the nucleus, these are joined because of the non-additive condition. This is mathematically equivalent to considering the loss as a separate character. With respect to the state allocation in the cladogram, it is equally parsimonious to consider state 1 as supporting node 3, then reversing in *Fulmentum*, or a convergence between *Nassodonta* and *Zemira*. The first hypothesis is shown in the Fig. 1.

Pallial organs

8. Siphon: 0 = long; 1 = short, almost inconspicuous (*Benthobia, Zemira*) (CI = 50; RI = 50).

The siphon is a modification of the mantle border and is distinct from the development of a siphon in the shell. There are taxa that possess a siphon in the shell, yet lack a developed siphon in the mantle, as, *e.g.*, Stromboidea (Simone 2005) and Cerithioidea (Simone 2001), while other taxa possess a well-developed siphon at mantle border, but lack any special modification in the shell, as, *e.g.*, Calyptraeoidea (Simone 2002). The long and exploratory pallial siphon is the rule in Hypsogastropoda, and is considered to be plesiomorphic in neogastropods. State 1 is considered a reduction.

9. Osphradium length relative to gill length: 0 = shorter than half (*Siratus*); 1 = longer than half (*Melapium, Fulmentum, Nassodonta*); 2 = almost same length (*Zemira, Benthobia*) (CI = 50; RI = 33; additive).

Although the states are optimized as additive, based on ontogeny, identical results and indices are produced when the character is considered not additive.

10. Osphradium: 0 = symmetrical; 1 = asymmetrical (*Benthobia, Nassodonta*) (CI = 50; R I= 50).

Symmetry refers to the left and right filaments being symmetrical about the axis of the osphradial gangilion, with the filaments of both sides similar sized. It is equally parsimonious to consider state 1 as convergent between node 2 and *Nassodonta*, or supporting node 1 and reverting in node 4; the first hypothesis is shown in the Fig. 1.

11. Osphradium with monopectinate anterior portion: 0 = absent; 1 = present (*Benthobia*) (CI = 100; RI = 100).

Osphradium characters (9-11) are normally connected to reduction in body size. The smaller the animal, the larger, proportionally, is the osphradium. The same can be concluded with regard to the asymmetry of the osphradium filaments. Smaller animals tend to have the left filaments smaller than the right ones. The loss of the left filaments (character 11) can be considered as the extreme of this tendency to miniaturization. In the case of *Benthobia*, the monopectinate condition is only present in the anterior portion of the osphradium (Simone 2003: figs. 7B, 9B, 11A, 12A).

Digestive system

12. Ventral chitinous platform within the oral tube: 0 = absent; 1 = present (*Melapium, Zemira, Siratus, Fulmentum*) (CI = 100; RI = 100).

The chitinous platform is a relatively thick longitudinal band located along the ventral surface of the oral tube. It starts close to the point where the odontophore enters the oral tube, and ends close to the mouth. This platform is particularly well developed in muricids that I have examined, but it is also present in the above listed other species (Figs. 7F, 15E: ol). The function of this structure is unknown, but normally the salivary glands open in the middle level of its lateral edges, which suggests a relationship between the glands and the chitinous platform. This reinforcement of the inner surface of the oral tube may possibly be linked to contact with the radular teeth, serving to avoid self-injury. There does not appear to be a direct relationship with the jaws, which are located on the dorsal surface of the oral tube, and are normally absent in neogastropods.

13. Length of odontophore horizontal muscle (m6): 0 = about half the length of the cartilages; 1 = almost

the same length as the cartilages (*Nassodonta, Fulmentum, Melapium, Zemira, Siratus*) (CI = 100; RI = 100).

The horizontal muscle (m6) connects both odontophore cartilages to each other along their ventral edge. In neogastropods, however, this muscle is normally thin and tends to become longer, almost as long as the cartilages. This feature is explored in this character (Figs. 6B, 12A, 16C-D, 19B).

14. Jaw muscle (mj): 0 = thin, as a flap; 1 = as a separate band (*Siratus, Zemira, Melapium, Nassodonta*) (CI = 50; RI = 66).

The jaw muscles (mj) are modified in neogastropods because of the greater development of the odontophore tube, which makes the connection between it and the oral tube. This modification may be responsible for the further alteration of state 1. Although the neogastropods normally lack jaws, as is the case in the species examined, this name is here maintained in order to indicate the homology of this structure with those of the remaining caenogastropods.

15. Odontophore ventral tensor muscle of radula (m11a-m4v): 0 = absent; 1 = present (all taxa in this study) (CI = 100; RI = 100).
16. Dorsal tensor muscles of radula m4 and m5: 0 = separated from each other; 1 = continuous with each other (*Siratus, Fulmentum, Melapium, Zemira, Nassodonta*) (CI = 100; RI = 100).
17. Connection of m4 with inner surface of cartilages: 0 = absent; 1 = present (*Siratus, Melapium, Fulmentum*) (CI = 100; RI = 100).
18. Odontophore cartilage outline: 0 = elliptical; 1 = elongated (*Siratus, Melapium, Nassodonta*) (CI = 50; RI = 50).
19. The odontophore of the muricoideans (broad sense) is different from those of the remaining caenogastropods in two main features. The first is the tendency to elongation, which results in odontophores that may be as long as the proboscis. They extend into the haemocoel when the proboscis is retracted. Another difference is the development of ventral tensor muscles of the radula. This muscle pair is present in archaeogastropods, but is practically lost in caenogastropods. The muricoideans revert to this condition, re-acquiring the ventral tensor muscles from a modification of the dorsal ones. The modifications resulting from these tendencies are explored in above characters (15-18). Odontophore tube connecting odontophore to the oral tube: 0 = absent or very short; 1 = long (all taxa in this study) (CI = 100; RI = 100).

The odontophore tube is a separate structure from the well-known "oral tube" (Simone 2003, fig. 7G: oo) (Figs. 15D, 18E: oo). This muscular tube connects the odontophore to the oral tube. Elongation of this tube is another common character of the muricoideans, in which the buccal mass structures become V-shaped, with the mouth at the vertex of this "V".

20. Esophageal origin: 0 = posterior to odontophore; 1 = anterior-dorsal to odontophore (buccal mass V-shaped) (all taxa in this study) (CI = 100; RI = 100).

In most caenogastropods, the buccal mass and esophagus are linear, *i.e.*, the origin of the esophagus is in the posterior region of the odontophore. As noted above, the buccal mass and esophagus may be V-shaped in the muricoideans, with the anterior esophagus and the elongate odontophore running parallel to each other.

21. Accessory salivary gland: 0 = absent (*Zemira*); 1 = paired (*Siratus, Melapium*?); 2 = unpaired (*Fulmentum, Benthobia*) (? = *Nassodonta*) (CI = 66; RI = 50; not additive).

As the accessory salivary gland has been considered as a synapomorphy of the Neogastropoda (Ponder 1974, Haszprunar 1988), its absence is considered plesiomorphic. This condition in *Zemira* is most likely a reversion. Kantor (1991) had considered, however, two apomorphic states of the accessory salivary gland, absent and the single (unpaired) condition.

The presence (state 2) in *Fulmentum* can be considered an autapomorphy for this taxon (convergent with node 2) or supporting node 5. The second hypothesis is shown in the Fig. 1, but in this hypothesis the pair of accessory salivary gland originated from a single gland.

22. Valve of Leiblein: 0 = absent; 1 = present (all taxa in this study) (CI = 100; RI = 100).
23. Valve of Leiblein oblique furrow: 0 = absent; 1 = present (*Zemira, Melapium, Fulmentum, Nassodonta, Siratus*) (CI = 100; RI = 100).

The valve of Leiblein is considered to be another synapomorphy of the Neogastropoda (Haszprunar 1988), and is certainly present in most muricoideans. As nothing similar can currently be attributed to the Conoidea, the presence of this valve is here considered to be an apomorphic state (character 22), supporting a branch uniting muricoideans and cancellarioideans. Its internal organization, on the other hand, has not been studied in detail. Comparisons at this level are very difficult, as information is inadequate. Certainly, the valve of Leiblein is a complex structure, the function of which is uncertain. In some species, the valve of Leiblein has a transverse furrow that can be considered as homologous to the bypass shown by Ponder (1974: fig. 3), a way for the food pass directly to the middle esophagus without passing through the valve. This condition is considered apomorphic (Figs. 7B, 12B, 15C), being one of the synapomorphies of the node 3.

24. Gland of Leiblein: 0 = absent; 1 = present (all); 2 = elongated (*Zemira, Melapium*) (CI = 66; RI = 0; additive).

The gland of Leiblein is another synapomorphy of the Neogastropoda (Ponder 1974; Haszprunar 1988). It is further modified in several taxa, including its disappearance and its modification into a venom gland in the conoideans. The modification explored here is the elongated form. In this pattern, the gland is stored inside the haemocoel intensely coiled. It is shown in Figs. 7C and 15B artificially uncoiled. The additive condition is based on ontogeny, as very young specimens possess a shorter gland, however, nothing changes in the result or indices if the character is considered not additive.

25. Gland of Leiblein duct: 0 = short; 1 = long (about half the length of the middle esophagus) (*Siratus, Zemira, Melapium, Fulmentum*) (CI = 100; RI = 100).
26. Gland of Leiblein duct: 0 = with transversal septa (*Siratus*); 1 = glandular (*Zemira, Fulmentum*); 2 = simple (*Melapium, Benthobia, Nassodonta*) (CI = 40; RI = 25; additive).

The gland of Leiblein characters (24-26) are based on the hypothesis that this gland is a modification of the middle esophageal gland, present in the higher mesogastropods (Naticoidea, Cypraeoidea, Tonnoidea). In these taxa, the esophageal gland consists of a series of transverse septa. Something similar is also found in some muricoideans, but reduced and located in the duct of gland of Leiblein, further supporting the link between these two structures. The presence of such septa in the gland duct is considered plesiomorphic. The glandular condition of the duct is considered as an intermediate step for a simple-duct condition. This is the reason for considering the states in an additive optimization; however, if considered not additive, the resulted cladogram is the same, but the indices change to CI = 50 and RI = 0.

27. Stomach form: 0 = a simple curve; 1 = with a dilated chamber posterior to esophageal insertion (*Fulmentum, Melapium, Zemira, Siratus*) (CI = 100; RI = 100).
28. Number of stomach ducts to the digestive glands: 0 = 2 (*Melapium*); 1 = 1 (*Benthobia, Fulmentum, Zemira, Siratus*) (?= *Nassodonta*) (CI = 50; RI = 0).

The stomach of normally carnivorous neogastropods, is, in most taxa, a simple curve. However, some taxa have developed a more complex stomach that is considered to be apomorphic herein. The number of the ducts leading to the digestive gland tends to be simplified, form a pair, as normal in lower caenogastropods, to a single duct.

29. Anal papilla: 0 = absent; 1 = present (*Siratus, Melapium, Fulmentum*) (CI = 100; RI = 100).

The anal papilla is not a conspicuous structure, but is present along the dorsal margin of the anus in above mentioned species (Figs. 10A, 14C: al), as well as in the remaining muricids examined. It most likely represents a synapomorphy.

Genital system

30. Penis duct: 0 = open (a furrow) (*Siratus, Melapium, Fulmentum*); 1 = closed (a tube) (*Zemira, Nassodonta, Benthobia*) (CI = 50; RI = 66).
31. Penis retractile terminal broad papilla: 0 = absent; 1 = present (*Benthobia, Fulmentum*) (CI = 50; RI = 50).

The male genital system is not normally well preserved, as most of the visceral structures are lost or not extracted without damage. This is the case of the present sample. However, comparisons were made among those species for which material was available. The opened condition (character 30) is considered plesiomorphic, based on the condition found in most basal caenogastropods, but the closed (tubular) condition commonly occurs throughout the caenogastropods as convergences.

32. Bursa copulatrix: 0 = a blind sac; 1 = terminal, as continuation of oviduct (*Benthobia, Fulmentum, Zemira*); 2 = absent (*Siratus*) (not additive) (CI = 66; RI = 0).

The polarization of this character is also based on the condition normally found in other caenogastropods, mainly higher mesogastropods. Although several interesting differences in the female genital system were found, all appeared to be autapomorphic, except for the condition of the bursa copulatrix.

Central nervous system

33. Nerve ring ganglia: 0 = ganglia separated; 1 = ganglia almost fused (all) (CI = 100; RI = 100).
34. Buccal ganglia: 0 = close to buccal mass; 1 = close to nerve ring (all) (CI = 100; RI = 100).

Both central nervous system characters are polarized based on the remaining caenogastropods, in such the ganglia are clearly separated from each other (character 33), and the paired buccal ganglia are located far from the nerve ring and closer to the buccal mass (34). Both conditions are further modified in the above mentioned taxa.

TAXONOMY

The cladogram based on the set of characters shown in the Table 1 is depicted in figures 1 and 2. Character polarity is based mainly on Tonnoideans, *i.e., Tonna galea* (Linné, 1758) and *T. maculosa* (Dillwyn, 1817) (Simone 1995), as well as other species still under study. Based on this scenario, the Conoidea share seven synapomorphies with the ingroup, the more important being determinate shell growth (character 3), the presence of the odontophore ventral tensor muscle of radula (15), the gland of Leiblein (character 24), closure of penis duct (character 30), and the adaptations of the nerve ring (characters 33, 34).

The ingroup also is supported by eight synapomorphies (**node 1**), the more important being the spiral furrow in the last shell whorl (character 1), the elongation of the osphradium (9), the odontophore tube (19), the valve of Leiblein (22), the further modification of the gland of Leiblein duct (26), and the reduction of the stomach ducts (28).

Node 2 represents the genus *Benthobia*, based on data from Simone (2003). Although five species had been studied, only two are included here because of the completeness of data. This node is supported by 9 synapomorphies, two are non-homoplastic: the posterior furrow of the foot (character 5) and the monopectinate condition of the anterior region of the osphradium (11). The features are convergent with other branches of the cladogram. Among the more notable are: the shortness of the siphon (8), the osphradium equal in length to the gill (9), a single accessory salivary gland (21) and the terminal papilla of the penis.

Node 3, the remaining ingroup, is supported by six synapomorphies, the more conspicuous are: the close situation of the cephalic tentacles (character 4), the sub-terminal condition of the opercular nucleus (7), the length of the horizontal muscle of odontophore (13), and the oblique furrow of the valve of Leiblein (23).

The next dichotomy separates the nassariid *Nassodonta dorri* from the remaining ingroup taxa (**node 4**). The taxonomy of the genus *Nassodonta* has been analyzed by Kantor and Kilburn (2001), who provided a history and additional comments.

However, there is a remarkable similarity in shell characters with the pseudolivid taxa. As pointed by Kantor and Kilburn (2001: fig. 13), *Nassodonta* also possesses a deep basal spiral furrow in the anterior region of body whorl, mostly associated with a labral tooth. On the other hand, the anatomical characters such as the radula and the degree of fusion between both odontophore cartilages clearly show the nassariid nature of the *Nassodonta*.

Node 4 is supported by five synapomorphies, the more interesting being: the tooth at outer shell lip (character 2) that reverts in the node 6, the ventral chitinous platform in the oral tube (12), further elongation of the duct of the gland of Leiblein (25) and the dilatation of the stomach (27).

Node 5 unites the remaining ingroup species except *Zemira australis*, and is supported by four synapomorphies, most noteworthy being the single accessory salivary gland (character 21) and the anal papilla (29).

Node 6 is supported by five synapomorphies, and unites *Melapium*, that mostly is considered a pseudolivid, with the muricid *Siratus senegalensis*. Of the synapomorphies for this node, the more important are the double condition of the columellar muscle (character 6) and the paired state of the accessory salivary glands.

Based on this scenario, the formal family Pseudolividae, in the present sense, is not monophyletic. Four of the included genera (*Benthobia, Zemira, Fulmentum*, and *Melapium*) are mixed with a nassariid (*Nassodonta*) and a muricid (*Siratus*). Although the studied set of species represents only a subset of the genera included in the Pseudolividae, it appears to be is sufficient to demonstrate the polyphyletic nature of the taxon. Since the type species of *Pseudoliva* Swainson, 1840, the type genus of the family Pseudolividae, *P. crassa* (Gmelin, 1791), was not studied, no definite conclusions about the taxonomy of Pseudolividae can yet be reached. However, at least the present concept of the family level taxon has been shown as lacking phylogenetic support.

Among the species studied, *Fulmentum ancilla* is closest to *Pseudoliva*. Some authors consider this species to belong to *Pseudoliva* (*e.g.*, Kantor 1991, Hayes 1994). If *P. crassa* is close to *F. ancilla*, the cladogram indicates that it, and with *Melapium*, could be considered as belonging to Muricidae or, at least, a sister taxon of that family. According to this tree topology, the genera *Zemira* and *Benthobia* could be placed in other families. Kantor (1991: 34) provided some anatomical information on *Pseudoliva zebrina* A. Adams, 1853, which shares similarities with *F. ancilla*, mainly with respect to foregut characters. This can further indicate a close relationship between *Fulmentum* and *Pseudoliva*.

The phylogenetic analysis by Kantor (1991: fig. 19) shows four synapomorphies supporting the monophyly of the Pseudolividae (except *Melapium*). Three of the synapomorphies (three teeth per radular row, a short free portion of the duct of salivary gland, and the anal gland) occur commonly in the Muricoidea. A fourth synapomorphy (accessory esophageal gland) is a distinctive character, but the variability of form and position of this gland, and its presence in several other muricoideans, suggest the possibility of convergence. While these four anatomical characters are the basis for recognizing the family Pseudolividae, none of them emerged as important synapomorphies in the present study. Similar arguments can be made with regard to the seven synapomorphies proposed for *Melapium* in that paper.

The outcome of the present analysis shows Pseudolividae, as currently understood, to be polyphyletic, contradicting previously published results, and indicating that the present concept of this taxon must be reevaluated. Most probably some of the genera now assigned to Pseudolividae will be found to belong to other families, while the name Pseudolividae is apparently only applicable only to the genera *Pseudoliva* and *Fulmentum*.

The definitions and limits of the families of the muricoideans only can be refined after a much wider analysis, including samples of much more representatives.

CONCLUSIONS

(1) The family Pseudolividae, in the present concept, is polyphyletic and must be not used as a formal taxon.

(2) Detailed morphology is valuable for comparative studies, as all examined species differ greatly in most structures.

(3) The genera *Zemira*, *Fulmentum*, and *Melapium* share synapomorphies with the genus *Siratus* (Muricidae). These taxa also share further synapomorphies with the *Nassodonta* (Nassariidae), being separated by them from *Benthobia*.

(4) No special taxonomical re-arrangement is proposed because of weakness of definition of the Muricoidea families.

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FIGURE CAPTIONS

In the figures, the following abbreviations are used: **aa**, anterior aorta; **ac**, auricle connection with kidney chamber; **ad**, accessory salivary gland duct; **ae**, accessory salivary gland; **af**, afferent gill vessel; **ag**, albumen gland; **al**, anal papilla; **an**, anus; **ao**, posterior aorta; **at**, vaginal atrium; **au**, auricle; **ba**, bursa copulatrix aperture; **bc**, bursa copulatrix; **bg**, buccal ganglion; **bm**, buccal mass; **br**, subradular membrane; **ce**, cerebral-pleural ganglia; **cg**, capsule gland; **cm**, columellar muscle; **cp**, capsule; **cv**, ctenidial vein; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **di**, diaphragm membrane separating haemocoel from visceral cavity; **ea**, anterior esophagus; **ef**, esophageal folds; **em**, middle esophagus; **ep**, posterior esophagus; **es**, esophagus; **ey**, eye; **fp**, female pore; **fs**, foot sole; **ft**, foot; **gi**, gill or gill filament; **gl**, gland of Leiblein; **gm**, gill muscle; **gp**, pedal ganglion; **he**, head; **hg**, hypobranchial gland; **in**, intestine; **ir**, insertion of m4 in tissue on radula (to); **is**, insertion of m5 in subradular membrane; **kc**, membrane between kidney and pericardium; **kd**, dorsal chamber of kidney; **ki**, kidney; **kl**, kidney dorsal lobe; **km**, membrane between kidney and pallial cavity; **kv**, ventral lobe of kidney; **ld**, duct of gland of Leiblein; **lg**, secondary gland of duct of gland of Leiblein; **m1** to **m14**, extrinsic and intrinsic odontophore muscles; **mb**, mantle border; **mc**, circular muscles of odontophore; **mf**, muscle fibers; **mj**, jaws, buccal, and oral tube muscles; **mo**, mouth; **ne**, nephropore; **ng**, nephridial gland; **nr**, nerve ring; **nv**, nerve; **oa**, opercular pad; **oc**, odontophore cartilage; **od**, odontophore; **of**, odontophore cartilage fusion; **oi**, opercular insertion; **ol**, oral tube ventral chitinous platform; **oo**, odontophore tube connecting to oral tube; **op**, operculum; **os**, osphradium; **ot**, oral tube; **oy**, ovary; **pa**, penis aperture; **pb**, proboscis; **pc**, pericardium; **pd**, penis duct; **pe**, penis; **pf**, penis furrow; **pg**, pedal glands anterior furrow; **pp**, penis papilla; **pt**, prostate; **pu**, pedal ganglion; **py**, pallial cavity; **ra**, radula; **rd**, seminal receptacle duct; **rh**, rhynchostome; **rm**, retractor muscle of proboscis; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **rv**, renal efferent vessel; **sa**, salivary gland aperture at oral tube; **sc**, subradular cartilage; **sd**, salivary duct; **se**, septum between esophagus and odontophore in buccal mass; **sg**, salivary gland; **sh**, shell siphon canal; **si**, siphon or siphon insertion; **sp**, supra-esophageal ganglion; **sr**, seminal receptacle; **st**, stomach; **su**, subesophageal ganglion; **sv**, seminal vesicle; **sy**, statocyst; **te** cephalic tentacle; **tg**, integument; **to**, tissue on middle region of radula preceding buccal cavity; **ts**, testis; **va**, vaginal duct; **vd**, vas deferens; **ve**, ventricle; **vf**, oblique furrow of valve of Leiblein; **vg**, visceral ganglion; **vn**, visceral nerve; **vl**, valve of Leiblein; **vo**, visceral oviduct.